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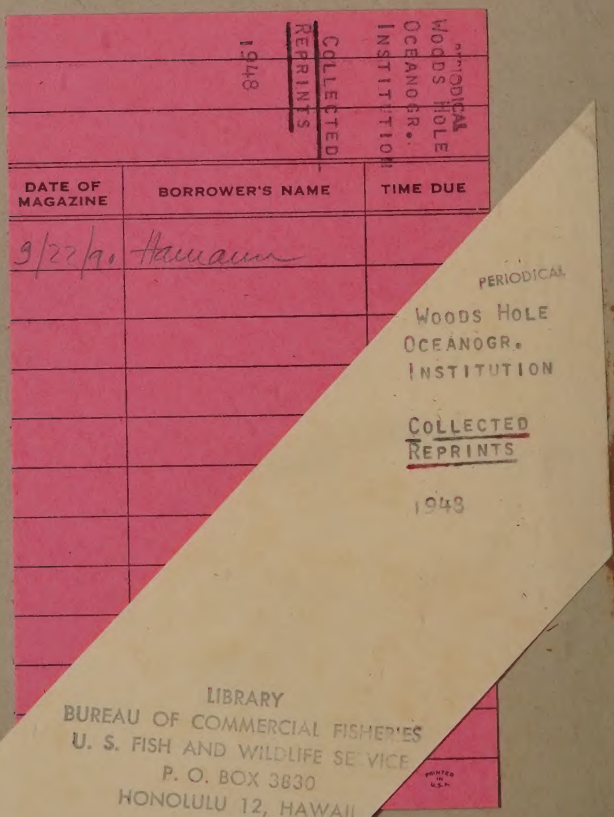

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Contribution No. 376

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE
Vol. 100, No. 2

FORAMINIFERA OF THE CONTINENTAL SHELF FROM THE GULF OF MAINE TO MARYLAND

By Frances L. Parker

With Seven Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
April, 1948

No 2. — *Foraminifera of the Continental Shelf from the Gulf of Maine to Maryland*[1]

By Frances L. Parker

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[1] Contribution No. 376. Woods Hole Oceanographic Institution.

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INTRODUCTION

GENERAL STATEMENT

This is one of two projected papers concerning the Foraminifera of the continental shelf of the western North Atlantic. It concerns that part of the continental shelf extending from the Gulf of Maine to Maryland. The sediments were collected under the direction of Henry C. Stetson of the Woods Hole Oceanographic Institution during several trips of the research ships *Atlantis* and *Asterias*. The samples were those used by Stetson in his study of the sediments of the continental

shelf. A description of the dredge used in obtaining the material and a discussion of the sediments may be found in his paper (Stetson, 1938).

The foraminiferal faunas from the bottom sediments have been studied in a quantitative manner and an especial inquiry has been made into the possibility of establishing faunal zones correlated to depth for different foraminiferal assemblages. Although a considerable amount is known about the general habitat of different genera and species of Foraminifera, such information is quite inadequate for attacking certain oceanographic and geologic problems. Detailed data on the depth ranges of these faunas on the continental shelf should be important in interpreting the more recent history of the ocean, as recorded in submarine cores. Moreover, if certain principles of faunal distribution can be established, such information should be of value in interpreting marine rocks of Cretaceous and Tertiary age.

It has been found that there are four definite faunal zones in the region studied. It is impossible, however, at the present time to give definite causes for this zoning, because of lack of knowledge concerning the habits and life histories of the living organisms. Few facts are known concerning the effect of temperature, salinity, and depth. Little is known of the nutritional requirements, migratory habits, and other factors. Certain physical features of the various zones studied have been indicated and some fairly reasonable hypotheses may be deduced from these. At the present state of our knowledge it is impossible, however, to determine with any precision the conditions which will produce a given assemblage.

ACKNOWLEDGMENTS

This work was made possible by the assistance and cooperation of the Woods Hole Oceanographic Institution. Particular thanks are due Messrs. Henry C. Stetson and Fred B. Phleger for their advice and suggestions throughout; to Dr. Joseph A. Cushman for his help in photographing specimens, to Constance French for drafting the figures, and to Miss Ellen Meehan for several drawings. Valuable help and criticism have also been given by Lloyd G. Henbest of the U. S. Geological Survey and Shepard W. Lowman of the Shell Oil Company.

LOCATION OF SAMPLES

The marine bottom samples used for the present study were taken in a series of traverses across the continental shelf out to, or slightly

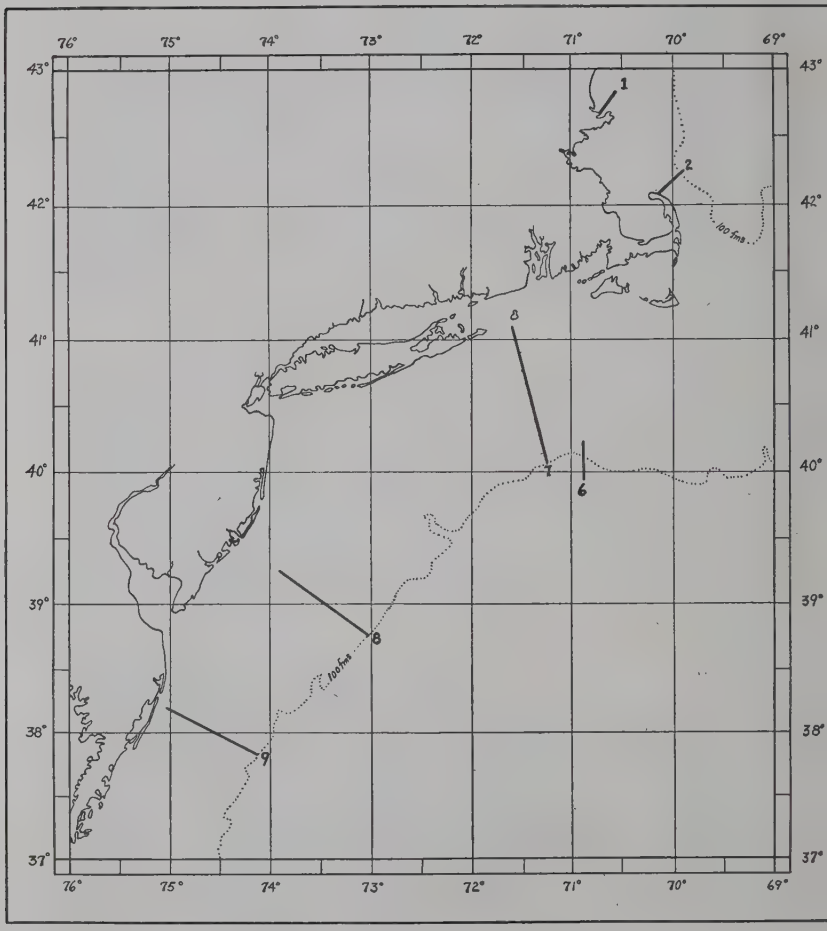

Figure 1. Map showing location of traverses.

beyond, the break in slope. The samples were taken at regular intervals, in most cases one mile apart (Stetson, 1938, pp. 41–44). There are four traverses south of Cape Cod located as follows: 71 miles south of Marthas Vineyard on a line beginning at 40° 11′ N, 70° 48′ W and running from 122 meters to 680 meters (series 6); 1¼ miles southwest of Block Island on a line running 167° from the whistling buoy and running from 19 meters to 200 meters (series 7); off the coast of New Jersey beginning at 39° 14′ N, 73° 54′ W and running offshore in a southeasterly direction from 46 meters to 610 meters (series 8); off the coast of Maryland, beginning at 38° 12′ N, 75° 02′ W and running offshore in a southeasterly direction from 22 meters to 386 meters (series 9). These lines cross the shelf from the very shallow water to the break in slope with the exception of the Marthas Vineyard traverse which starts at its northern end at a depth of 122 meters. There are two short traverses in the region east and north of Cape Cod: on a line running 46° from the beach at Cape Cod Light from 12 meters to 203 meters (series 2); on a line running 35° from can buoy No. 1 at entrance to Essex River, Ipswich Bay, Mass., from 9 meters to 71 meters (series 1). A total of 86 samples were studied, 70 of which have been included in the faunal tables.

METHOD OF STUDY

GENERAL STATEMENT

An attempt has been made to give the facts concerning the occurrence of Foraminifera in a manner which will easily lend itself to analysis and interpretation. A study of the various faunas involved showed that some way of simplification would have to be devised to make it possible to deal with the great abundance of material. In order to do this the different species have been counted and their relative abundances determined on a percentage basis. The actual abundance of Foraminifera has also been estimated for samples of standard size. Many rare forms have been necessarily omitted and in samples containing a very high percentage of Foraminifera many occurrences, which from their abundance seem to be important, have been found to be of small significance. Species occurring with a percentage of less than 0.1% have been omitted from the tables and very occasionally species occurring in higher percentages, if they appear to be of no significance. A few rare forms which do not appear in the tables have been listed separately when they have occurred persistently in several

samples and when they seem to have a definite value in zonal analysis. By this procedure it has been possible to cut down the working fauna from about 300 species to about 150. The danger of drawing conclusions from spotty occurrences of species in small numbers also has been eliminated.

The value of the percentage method in presenting the facts lies in the ease with which a definite analysis can be made of the relative importance of the various species in the different samples. This cannot be done if species are merely listed as common, rare, etc. In many cases it was found that samples having comparatively few specimens showed similar percentages of the various species as did a rich sample. For the sake of brevity and to avoid needless repetition the data of only part of the samples studied is given in the accompanying tables. Zonal changes were so gradual and often so many samples showed exactly similar conditions that it seemed unnecessary to give the listings of all of them. These samples served as a useful check, however, and helped to bring to light abnormalities due to localized conditions.

TREATMENT OF SAMPLES

In order to give a rough estimate of the actual abundance of the Foraminifera in a sample, a standard amount of 100 cc. of sediment was used. In cases where this amount was not available, or the silt and clay had been previously sieved out for mechanical analysis, computations were made to standardize the results. The material was treated with carbon tetrachloride according to the method developed by Dr. Ozawa at the Cushman Laboratory (Cushman, 1940, p. 27). In some cases it was found that an appreciable percentage of the forms had not floated due to their large size or due to the thickness of the test walls. In such cases the residues were examined separately and the figures included with those of the floated sample. In most cases these figures did not materially change the percentage figures already determined, but the ratios were considerably changed in samples where such forms as *Marginulina bacheii* Bailey[1] and *Gaudryina* (*Pseudogaudryina*) *atlantica* (Bailey) were found.

In counting the specimens, flotations smaller than 0.1 cc. in volume could be used in their entirety and total counts made. For larger samples a simple apparatus to divide the material was devised. This consisted of a tray four inches square divided in the middle by a brass

[1] A list of species giving plate and figure numbers will be found on page 237.

partition whose upper edge had been ground to a knife edge. A trough with a v-shaped cross section was soldered to this partition at an angle of forty-five degrees. The lower end of the trough was split so that the sides could extend down on either side of the brass partition. The material was allowed to slide down the trough and was divided into approximately two parts by the knife edge. In this way it was possible to divide the samples many times without getting unequal divisions of the different grade sizes, even when the divisions were extremely small. The accuracy of the divisions was checked by counts and the percentage differences were found to be very small. In all cases where it was found necessary to divide the sample, two aliquots were taken, one from divisions made using one side of the apparatus and one from those using the other. Parallel counts were made and the results of the two averaged. In this way errors that might result from faulty division due to the lack of precision of the apparatus were reduced. Each sample was weighed before division and the resulting aliquots weighed after counting, so that an estimate of the actual abundance of the species could be made.

Over 300 species were identified from all the samples studied, but of these only about 150 were found to be useful in the problem at hand. Counting and calculating each rare species separately was found to be a waste of effort in most cases. Such species were included under "miscellaneous forms." A preliminary examination of the entire sample is a useful guide to the relative importance of the various species. In the present instance the different species were picked out from small samples and a preliminary list of the significant forms compiled. The time involved in doing this is great, however, and once the worker is familiar with the fauna it is not necessary.

It should be realized that the figures obtained by this procedure, no matter how much care is taken, are subject to error. The methods are necessarily rough from the initial sampling to the exact counting of the specimens and it would seem absurd to give actual figures, especially in the case of the estimates of the total numbers of Foraminifera to be found in a sample. For this reason the actual abundance is given in an estimated round number which should be regarded only as an approximation. The actual percentage figures computed are given, but here also some latitude should be allowed. This is especially true of samples where the planktonic forms make up a large proportion of the material. In order to get a fair representation of benthonic forms it was necessary to count a fairly large aliquot.

In working out the percentages the planktonic forms were separated

from the benthonic. This has not been done by most authors, but it seems necessary in view of the fact that at least two different environments are represented and a mixture of these elements would give an untrue picture of the facts, biologically, and lead to a false interpretation. For want of more complete data, the conventional list of planktonic forms has been used. It is probable, however, that certain planktonic forms may have bottom-living stages and even more probable that bottom-living ones have planktonic, or semi-planktonic, stages. The possibility that zoospores may be carried considerable distances should be kept in mind. These are added complications which must be minimized at the present stage of our knowledge.

FAUNAL ZONES

GENERAL STATEMENT

In discussing the zoning of the Foraminifera on the continental shelf, it is necessary to divide the area into two parts. The first part includes the region from Maryland to Cape Cod, the second that east and north of Cape Cod. It is interesting to note that Cape Hatteras forms the boundary of yet a third faunal region. Within these regions more or less similar conditions prevail, but there is a marked difference between the faunal characteristics of the regions. Since the sampling south of Cape Cod has been more widespread and complete, the findings in that region will be used as a gauge for those in the northern. Definite bathymetric limits are given for the zones, but these should be considered as only approximate. In the discussion of the zones only the benthonic fauna is considered.

The identifications of the species have been taken chiefly from Cushman's monograph of the Foraminifera of the Atlantic Ocean (Cushman, 1918–1931). Some of these identifications are probably not up to date, but since it is not the purpose of this paper to give a strictly faunal study it has seemed more practical to use the names which have become familiar with usage. Many of the genera, which have been re-named in more recent studies, have been changed to conform with the later classifications; in some places where it has seemed expedient species names also have been corrected. All the species listed have definite percentage ratings of one-tenth of one per-cent, or more, in the samples unless specifically designated as *rare*. They do not necessarily appear in every sample of a zone, but are nevertheless considered to be diagnostic.

REGION FROM CAPE COD TO MARYLAND

Zone 1. 0—15 Meters

This includes the littoral and sub-littoral zones. The traverses do not penetrate this zone, but material has been collected in Buzzards Bay in different types of sediment. Since Dr. Cushman is planning a detailed study of this fauna, only a few general points will be indicated. The samples taken in sand yield the richest fauna. Various species of *Elphidium* form the bulk of the samples, with *Rotalia beccarii* (Linnaeus), *Quinqueloculina seminulum* (Linnaeus), and *Eggerella advena* (Cushman) present in appreciable quantities. Samples taken in mud show a very few *Quinqueloculinas* and *Guttulinas* with a slightly higher percentage of *Eggerella advena*. Definite counts have not been made of this material and for the reasons given above no detailed study has been made. In general it may be said that bottom samples of the littoral zone would probably show a very high percentage of *Elphidium* throughout this area.

Zone 2. 15—90 Meters

The 15 meter limit given to the inner edge of this zone is subject to some qualification. None of the samples taken in the traverses were from depths shallower than 19 meters. The depth of 15 meters has been chosen for the inner limit of Zone 2 in open ocean conditions, since this depth is well below the tide level and at a sufficient distance from the shore. Samples taken in an enclosed bay at this depth, however, may differ materially, as was shown when material taken at 19 meters south of Block Island was compared with that taken in 17 meters in Buzzards Bay.

The following species were found in the Maryland, New Jersey, and Block Island traverses in Zone 2 only:

Quinqueloculina seminulum (Linnaeus)

Triloculina sp. (extends somewhat into Zone 3 in the Maryland traverse)

Eggerella advena (Cushman) (occurs in the first sample in Zone 3 of the Maryland traverse)

Globulina inaequalis Reuss var. *caribea* d'Orbigny (first sample of Zone 3 in Maryland traverse)

Trochammina lobata Cushman

Bolivina pseudoplicata Heron-Allen and Earland (found in 3 samples in Zone 3 of the Maryland traverse, at very low percentages)

The following species were found in abundance in the Maryland and New Jersey traverses, but occurred only rarely in the one off Block Island:

Globulina inaequalis Reuss
Cibicides concentrica Cushman

The following species were found with percentage rating in the Maryland traverse, but occurred only rarely in the New Jersey and Block Island traverses:

Nonion sloanii (d'Orbigny)
Elphidium sp.
Quinqueloculina seminulum (Linnaeus) var. *jugosa* Cushman
Pyrgo striatella (Cushman)

Discorbis sp. 2 and *Buliminella elegantissima* d'Orbigny were found only in the Maryland traverse. *Angulogerina* sp. 1 was found off New Jersey and rarely off Maryland.

Haplophragmoides major Cushman occurred only in the Block Island traverse with a single specimen found in each of the others.

It is interesting to note the occurrence of *Poroeponides lateralis* (Terquem) in the shallowest sample taken off Block Island, in 19 meters. This species has hitherto only been recorded from the littoral zone in this part of the Atlantic, which suggests that this sample was taken near the transitional point between the first two zones. The species occurred rarely at 37 meters.

Ammodiscus sp. was found only in this zone, occurring rarely in all three traverses.

Of the species given above *Quinqueloculina seminulum*, *Eggerella advena*, and *Triloculina* sp. have the highest percentages. As a study of the tables will show, however, they never form, taken together, more than 30% of a sample and usually considerably less. The species, in addition to these, which form the bulk of the samples, with of course some variation between traverses, are: *Proteonina difflugiformis* (H. B. Brady), *Elphidium subarcticum* Cushman, *Elphidium incertum* (Williamson), *Cibicides refulgens* Montfort, *Elphidium* sp. found in quantity only in the Maryland traverse, *Guttulina lactea* (Walker and Jacob), *Eponides frigida* (Cushman) var. *calida* Cushman and Cole. *Bulimina marginata* d'Orbigny appears at high percentages at the deeper end of the zone. The species given above do not necessarily reach their highest percentages in this zone, but do form a large proportion of the samples when taken together. As it was very difficult to differentiate the broken off chambers of *Reophax scorpiurus* Montfort from the specimens of *Proteonina difflugiformis* and as neither form

appeared to have any great significance in this study, no attempt was made to separate them and they are listed together under the latter name. It is interesting to note that *Cibicides refulgens* reaches its highest percentages at 60–70 meters in the Maryland and New Jersey traverses, but does not even appear in the Block Island samples in material shallower than 117.7 meters, except rarely.

Zone 3. 90—300 Meters

All four traverses in the Cape Cod to Maryland region penetrate this zone. It was possible to fix the outer limit fairly closely in the short traverse taken south of Marthas Vineyard. The change occurs between the 228 meter sample and the 300 meter sample. In the New Jersey and Maryland lines, consecutive samples go from 154 to 386 meters and 182 to 610 meters respectively, so that in these traverses it was impossible to define the limits of the zones very closely. The Block Island traverse ends at 200 meters and, therefore, does not penetrate the fourth zone. The third zone has the richest benthonic fauna both in actual abundance and in number of species found. An example of this may be seen in the Lagenidae, which are confined almost entirely to this zone and of which there are present at least 100 species, some of them occurring rarely but others in great numbers. The group as a whole sometimes forms as much as 25% of a sample, although, as a rule, it forms about 5%. In zone 4 this percentage drops to 1% or less. The larger proportion of the species occur rarely and cannot be considered separately, but taken together they become of considerable importance. In the tables these rare species have been counted together and grouped under "miscellaneous Lagenidae."

The following species are confined to Zone 3:

Gaudryina (*Pseudogaudryina*) *atlantica* (Bailey)
Pseudoclavulina novangliae (Cushman)
Massilina sp.
Pyrgo cf. denticulata (H. B. Brady) (rare in Marthas Vineyard and New Jersey traverses)
Robulus sp. 1 (rare in the Maryland traverse) [1]
Robulus sp. 2
Robulus sp. 3. (rare in New Jersey traverse)
Marginulina bacheii Bailey
Miscellaneous Lagenidae (extend somewhat into Zone 4)

[1] Owing to the great confusion existing in the nomenclature of this genus, no attempt has been made to give the species definite names.

Nonion grateloupi (d'Orbigny) (rare in the Marthas Vineyard traverse)
Nonion cf. *barleeanum* (Williamson) (rare in the New Jersey traverse)
Nonionella turgida (Williamson)
Virgulina compressa (Bailey)
Gyroidina soldanii d'Orbigny (rare in the Maryland traverse)
Discorbis bertheloti (d'Orbigny) (rare in the New Jersey and Maryland traverses)
Eponides sp. (rare in the Block Island and New Jersey traverses)
Eponides umbonata (Reuss) var. *ehrenbergi* (Bailey) (rare in the Maryland traverse)
Epistomina elegans (d'Orbigny)
Cassidulinoides bradyi (Norman) (occurs in one sample in Zone 4 in the Marthas Vineyard traverse)
Planulina foveolata (H. B. Brady)
Textularia goessi (Cushman) (?) (occurs only in the Block Island and Marthas Vineyard traverses. It is found rarely in one sample of the Maryland traverse)
Cancris sagra (d'Orbigny) (rare in Marthas Vineyard and Block Island traverses)
Pulvinulinella cf. *exigua* (H. B. Brady) (rare in Marthas Vineyard and Block Island traverses)

The following species are confined to this zone and occur in some abundance although they form a negligible percentage of the samples and are, therefore, considered to be "rare."

Textularia pseudotrochus Cushman
Textularia candeina d'Orbigny
Karreriella affinis (Fornasini)
Pyrgo subsphaerica (d'Orbigny)
Trochammina globigeriniformis (Parker and Jones)
Pseudopolymorphina atlantica (Cushman and Ozawa)
Chilostomella ovoidea Reuss (does not occur in the New Jersey traverse)

Plectina apicularis (Cushman) and *Robertina* sp. are found only in the Block Island and Marthas Vineyard traverses. They occur rarely with the exception of one occurrence of the former off Block Island.

The following species occur in other zones but reach their percentage peaks in Zone 3:

Cassidulina laevigata d'Orbigny
Cassidulina crassa d'Orbigny (rare in the Block Island and Marthas Vineyard traverses)

Cassidulina sp. (rare in the Marthas Vineyard traverse)
Angulogerina angulosa Williamson (reaches its peak in Zone 4 of Maryland traverse)

Zone 4. 300—680 Meters

The data available at the present time are insufficient to fix the outer limit of this zone. Phleger (1942, p. 1081) places it between 600 and 1000 meters. The most noticeable change there is the greatly increased abundance of *Uvigerina peregrina* Cushman, which in many samples forms a very high percentage of the benthonic fauna. None of the samples of the traverses, the deepest of which was taken at 680 meters, penetrated a fifth zone.

Zone 4 is best represented in the Marthas Vineyard traverse. The Maryland and New Jersey traverses each penetrated it at one station. The zone is not represented in the Block Island series.

The fauna of this zone is not so rich in variety of species having a definite percentage value as is that of Zone 3. For this reason the list of forms confined to it is much shorter than that of Zone 3. The species found in this zone only are:

Listerella nodulosa (Cushman) (occurs in the last station of Zone 3 in the Marthas Vineyard traverse)
Ammosphaeroidina sphaeroidiniformis (H. B. Brady) (rare in New Jersey and Maryland traverses)
Bulimina exilis (H. B. Brady) (rare in Maryland traverse)
Bulimina marginata d'Orbigny var.
Gyroidina orbicularis d'Orbigny
Valvulineria sp. (rare in the Maryland traverse)

The following forms were found only at the two deepest stations, 610 and 680 meters, occurring only rarely at the former:

Nonion grateloupi (d'Orbigny) var.
Angulogerina angulosa (Williamson) var.
Uvigerina peregrina Cushman

Cassidulina norcrossi Cushman occurs in Zones 3 and 4 but reaches a much higher percentage in Zone 4.

The following species occur in Zones 3 and 4 but not in Zone 2:

Bolivina subaenariensis Cushman
Eponides umbonata (Reuss)
Bulimina (*Desinobulimina*) *turgida* Bailey
Uvigerina sp.
Uvigerina peregrina Cushman var. *bradyana* Cushman
Cassidulina sp. (does not occur in the Marthas Vineyard traverse)

The following species occur rarely and are confined almost entirely to Zone 4:

Valvulina conica Parker and Jones (0.7% at 610 meters in New Jersey traverse)
Karreriella bradyi (Cushman)
Pseudoglandulina occidentalis (Cushman)
Bolivina subspinescens Cushman (found at 610 meters and 680 meters; only single specimens found elsewhere)

REGION EAST AND NORTH OF CAPE COD

In the region east and north of Cape Cod a very different assemblage is found from that occurring between Cape Cod and Maryland. The fauna is much less rich in species and many species which occur only rarely in the southern region form high percentages of the samples. A few species are found which occur only in this region. The chief difference, however, in the faunas of the two regions lies in the absence in the northern of a large number of the forms found in the southern.

It is impossible to divide this region into definite zones. Various zonal distinctions can be made in the two traverses, but there is no apparent correlation between them. This may be due in part to insufficient sampling and the comparative shortness of the traverses (Cape Cod Light traverse—13 miles; Ipswich Bay traverse—6 8/10 miles). It is more probably due to the physical characteristics of the region. In the discussion of the temperature conditions found in the various zones, given later in this paper, it will be shown that definite correlations can be made between temperature conditions and zonal changes. In the northern region these temperature differences are not so sharply defined as they are in the southern. This is due to the complete breakdown of the stability of the water during the winter months throughout the region in which the traverses were made.

Cape Cod Light Traverse

A close analysis of Table 5 shows that there is some suggestion, at least, of zoning in this traverse. It is impossible, however, to give any exact limits to the zones.

The first station at the inner end of the traverse, located ½ mile from shore at a depth of 5 meters, has been omitted from Table 5. This is due to the unusual assemblage found. Various species occurred which were not found elsewhere in the traverse or in the whole northern

area. These species, many of them planktonic forms in poor condition, were typical of the area south of Cape Cod and it is probable that they were carried to their present location by the strong tidal current which runs along the shore. Further evidence of the presence of strong currents is found in the 12, 32, and 48 meter samples, all of which contain a very small number of Foraminifera. Stetson points out (1938, p. 18) that in the area covered by this traverse there is strong evidence that the bottom has been scoured out to a depth of 70 meters. This fact may account for the scarcity of forms found, and the supposition is that the shallow, 5 meter sample was taken in a location where for some reason the load of material being carried north was deposited.

The first sample to be considered is that taken one mile from shore at a depth of 12 meters. This sample probably lies in the sub-littoral zone. Only 18 specimens were found, representing 8 species. Of these 5 do not appear elsewhere in the traverse (with the exception of one specimen), 4 are attached forms, two species of the genus *Discorbis* and two of the genus *Trochammina*, and are of the type usually associated with a littoral assemblage.

In the section of the traverse from 32 meters to 121 meters, several species having definite percentage ratings are found which are typical of Zone 2 in the area south of Cape Cod. They are:

Haplophragmoides major Cushman (32-144 meters)
Eggerella advena (Cushman) (12-121 meters)
Quinqueloculina seminulum (Linnaeus) (12-48 meters)
Trochammina lobata (Cushman) (70-85 meters)
Ammodiscus sp. (occurs rarely 85-145 meters)

In the section of the traverse from 145-203 meters various species are found which occur only in Zones 3 and 4 farther south. They are:

Valvulina conica Parker and Jones (91-203 meters) (Zone 4)
Triloculina tricarinata d'Orbigny (rare 145-203 meters) (Rare—Zone 4)
Pseudoglandulina occidentalis (Cushman) (Rare—203 meters) (Zone 4)
Bulimina exilis H. B. Brady (rare—203 meters) (Zone 4)
Bolivina subaenariensis Cushman (145-203 meters) (Zones 3 and 4)
Cassidulina norcrossi Cushman (203 meters) (Mostly Zones 3 and 4)
Eponides umbonata (Reuss) (rare 144-203 meters) (Zones 3 and 4)

Astrononion stellatum Cushman and Edwards occurs practically throughout this traverse but it is almost entirely confined to Zones 3 and 4 in the southern area, where it is of rare occurrence.

A number of species which seem to have no zonal significance in the southern region are also found occurring practically throughout this traverse:

Proteonina difflugiformis (H. B. Brady)
Elphidium subarcticum Cushman
Eponides frigida (Cushman) var. *calida* Cushman and Cole
Cassidulina laevigata (d'Orbigny)
Cibicides refulgens (Montfort)

Ipswich Bay Traverse

This traverse is very short and has a comparatively limited fauna. It does not penetrate into a possible third zone. The first sample taken in 9 meters, close to the mouth of the Ipswich River, has a limited fauna which has no definite littoral characteristics. Several species typical of Zone 2 of the southern region are found throughout the traverse. They are:

Eggerella advena (Cushman)
Haplophragmoides major Cushman (37-71 meters)
Trochammina lobata Cushman (absent at 71 meters)

The bulk of most of the samples is made up of *Proteonina difflugiformis* and *Eggerella advena*. They form between 65% and 85% of the samples.

RELATIONSHIP OF FAUNAS TO PHYSICAL CONDITIONS

GENERAL STATEMENT

The zoning of the region between Cape Cod and Maryland appears to be a direct function of depth. The relationship between zoning and depth is not so clear in the northern area, east and north of Cape Cod, although here too there is some indication of faunal change with depth. There are many physical factors of the ocean water and the ocean bottom which are dependent, to a greater or less extent, upon depth, and the problem is to ascertain which of these are most influential in bringing about the faunal changes of the Foraminifera—in this case especially those of the bottom-living forms. It is necessary to consider such things as light, salinity, temperature, food supply, and sedimentation. It is possible that aeration and pressure also play an important part at times, but in the comparatively shallow depths and open sea conditions with which this paper is immediately concerned these factors are probably of minor importance.

LIGHT PENETRATION

The influence of light can have no direct bearing on the bottom-living Foraminifera except in the littoral zone and Zone 2. Indirectly, of course, it may be important in influencing the food supply of the forms living in the deeper zones. The majority of the species of the Foraminifera live well below the level of maximum light penetration (in measurable quantities). In the shallow depths a few cases have been noted of certain species living commensally with algae (Cushman, 1940, p. 11). George L. Clarke (1936) has made some measurements of light penetration in the western Atlantic and the following table shows some of his findings.

	Red	Green	Violet	Depth of Photosynthesis
Vineyard Sound	13 M	21 M	21 M	
Woods Hole Harbor	13 M	16 M	14 M	18 M
South of Cape Cod (moderate sea)		50 M		
Gulf of Maine	20–25 M	20–75 M	55–60 M	40 M

This table gives the depths of penetration of light of various wavelengths within the visible spectrum and the depth of photosynthesis at two stations. The conditions in the Gulf of Maine approximate those of the coastal water well out on the continental shelf, while the Vineyard Sound and Woods Hole findings are typical of inshore water (Clarke, 1936, pp. 4, 5). Woods Hole Harbor and the Gulf of Maine represent the two extremes and here we find photosynthesis possible down to depths of 18 meters and 40 meters respectively. The compensation point is somewhat less than this: 7 meters in Woods Hole Harbor and 24-30 meters in the Gulf of Maine (Clarke, 1939, p. 36).

TEMPERATURE

Temperature conditions can apparently be closely correlated with zoning. The northern and southern regions will be considered separately. Figure 3 gives the minimum and maximum bottom temperature curves for a profile extending southeast from Montauk Point, Long Island. The temperatures given in the figure have been taken from a series of temperature sections, plotted for various months in the year, made by Columbus O'D. Iselin of the Woods Hole Oceanographic Institution. He says that they may be taken as characteristic of the continental shelf throughout this area (Personal communication).

Using these figures, together with additional data given by Bigelow (1933) for the temperature conditions found in the southern part of the Cape Cod-Maryland region, we find that the approximate temperatures to which each zone is subjected are as follows:

Zone 1 0M–15M	0°–22°C (Vineyard Sound)
	0°–27°C (Chesapeake Bay)
Zone 2 15M–90M	3°–16°C (at 50 M the minimum is 6°C)
Zone 3 90M–300M	9°–13°C (at 300M the maximum is 10°C)
	(at 300M the minimum is 7°C)
Zone 4 300M–1000M	6°–8°C (350M)
	5°–6°C (600M)

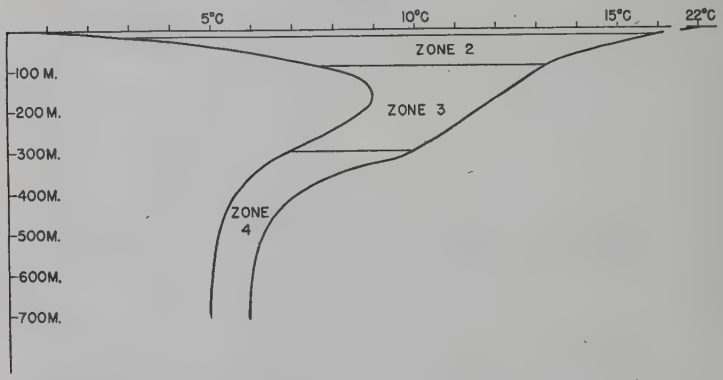

Figure 3. Maximum and minimum bottom temperatures in relation to depth on a profile running southeast from Montauk Point, Long Island.

Some interesting relationships may be found between the faunas living in the various zones and the temperatures to which they are subjected. The fauna of the first zone must be able to withstand not only very high and very low temperatures but also a high degree of temperature variation annually, which may easily account for the meager variety of species found. The second zone is subjected to a considerable variation of temperature also, although the variation is only about half as great as that found in the first zone. The minimum temperature in this zone is very low but somewhat higher than that of Zone 1. In the third zone, however, the minimum temperature is at its highest and the annual variation is not more than 5°C. This zone

contains the richest fauna, both in variety of species and to a lesser extent the actual abundance of the forms. The mean temperature of the fourth zone is somewhat lower than that of the third but the annual variation is slight, amounting to only 1° or 2°C.

There are two factors to consider in dealing with the influence of temperature on the Foraminifera. The first is the actual minimum and maximum temperatures to which a fauna is exposed and to which it must adapt itself, the second is the annual variation to which the fauna is subjected, which varies to some extent in different years. It seems obvious that fewer forms could adapt themselves to a wide range of temperature than to a narrow one. It also seems probable that many forms could be acclimated to higher or lower temperatures if the annual variation were not very great. This may be true of the species which are found to occur throughout the third and fourth zones.

It is interesting to note in this connection that the forms composing the main part of the fauna in the second zone and, to a somewhat lesser extent, the first are found throughout the four zones. There can be no doubt that these species are adapted to widely varying temperature conditions. On the other hand, some explanation other than temperature conditions may be found for the occurrence of forms peculiar to the first and second zones within, of course, the temperature limits found in the area. It is possible, however, that these forms need the high temperatures of the summer months to carry on their reproductive processes. Myers (1935) found in working with *Patellina corrugata* Williamson, a species restricted to warm, shallow waters of the littoral zone, that the maximum rate of reproduction occurred at 21°C. Below 18°C reproduction was retarded and above 25°C reproduction became abnormal. These findings were made, of course, under laboratory conditions but it is probable that analogous behavior would be found in the sea. Myers adds that in the winter months few developmental stages of this species were found.

In the area east and north of Cape Cod different conditions prevail. At the depths from which the samples were taken there is complete mixing of the water in the winter months. In addition the warming of the water in the summer is not as great as that further south. In the vicinity of the Cape Cod Light traverse the bottom temperatures at 50-100 meters vary from 2°-17°C; at 100-200 meters from 4°-9°C. In water shallower than 50 meters the temperature may drop below 1°C in the winter and in the summer may be slightly higher than 17°C.[1]

[1] These figures were obtained by the *Atlantis* on a series of cruises made in 1933 and 1934.

Similar conditions prevail in the Gulf of Maine, at least as far as the minimum temperatures are concerned, although the maximum temperatures are lower. This wide annual variation of temperatures and the low mean temperature provide what seem very adequate reasons for the absence in the Cape Cod Light traverse of the rich fauna found in Zone 3 further south. These facts also give a possible explanation of why the species found in the deeper water of this traverse are those which are common to both Zones 3 and 4 or are found only in Zone 4. The minimum temperatures encountered more closely approximate those found in Zone 4 further south, while the range of temperature variation of 6°C more nearly approximates that of Zone 3. The conditions combine, then, characteristics typical of Zones 3 and 4 in the southern area. If this explanation of the fauna found in this traverse is true, it shows that the minimum temperatures to which a fauna is subjected are of great importance. The fauna found bears more resemblance to that of the fourth zone than that of the third, although the maximum temperatures are higher and the range of temperature therefore greater.

SALINITY

Aside from localized brackish water conditions, met with in enclosed bays and near the mouths of rivers, there is comparatively little average salinity change to be met with at the bottom of the continental shelf water. The greatest variation is, of course, near shore and it becomes progressively less out to deep water. The salinities to be found at the various depths have been compiled from data given by Bigelow and Sears (1935). The values given are the maximum and minimum values that might be encountered over a period of years.

20 meters	31.4–33.6 o/oo
30–60 meters	32.3–33.6 o/oo
60–100 meters	32.8–34.6 o/oo
100–240 meters	34.6–35.5 o/oo
300 meters	34.9–35.7 o/oo

Whether these variations are large enough to affect the fauna can be a matter of speculation only at the present time. Zone 2 is subjected to a variation of 3.2 o/oo with a mean value of 33 o/oo; Zone 3 to a variation of 1.1 o/oo with a mean value of 35.2 o/oo. In Zone 4 the values are close to 35 o/oo.

Owing to the close relationship between temperature and salinity, it is impossible to determine which is the more important influence on

the fauna or whether, as is more probable, it is the combination of the two which is effective. Laboratory experimentation is probably needed for the solution of this problem.

FOOD SUPPLY

At the present time nothing of importance can be said concerning the nutrition of the Foraminifera as it relates to this problem. They are generally supposed to subsist on diatoms, algae, and other vegetable matter. There can be no doubt that at different times of year food of this sort is more scarce on the continental shelf than at others. Whether the relative scarcity of the supply would materially affect the Foraminifera cannot be said until further work on the living organisms has been done.

ABUNDANCE OF SPECIMENS

There is no apparent explanation of the great variations in the number of Foraminifera found in the samples. It was thought that there might be some correlation between the type of bottom sediment and the abundance of the Foraminifera. Such does not appear to be the case, however. Abundance curves were drawn and compared with the percentage curves of clay, silt, and colloid in various traverses. There is no apparent correlation. Neither is there any significant relationship between the abundance curves of the Foraminifera and the relative percentages of gravel and sand. In general it may be said that there is an increase in the abundance of Foraminifera from the shallow water to the deeper. In the samples taken in less than 50 meters the total abundance was very low, being less than 0.1 cc. of Foraminifera to 100 cc. of raw material. This may be due in part to the scouring of longshore currents. It has been found that wave action does not materially affect the sediments beyond the 70 meter depth, and this fact may have considerable bearing on abundance. Another generalization that may be made is that the Foraminifera seem to be more abundant in the warmer areas. The samples in Zone 3 are richer on the average than those of other zones, although even here unexplained fluctuations take place.

It is possible that there are various mechanical agencies at work causing localization of rich and poor areas. Sorting mechanisms must act on the dead tests of Foraminifera as well as on the inorganic sediments. The rate of sedimentation may also vary. An argument in favor of the action of some sort of mechanical agency is that the relative

percentages of planktonic and benthonic Foraminifera remain the same, or at least maintain their relative relationships in view of their position on the continental shelf, regardless of whether the sample has a relatively large or small number of organisms in it. If the abundance of Foraminifera in a sample were due to some cause other than mechanical sorting or the differential rate of sedimentation one would expect a change of ratio between planktonic and benthonic faunas as they are not affected by the same local environmental conditions.

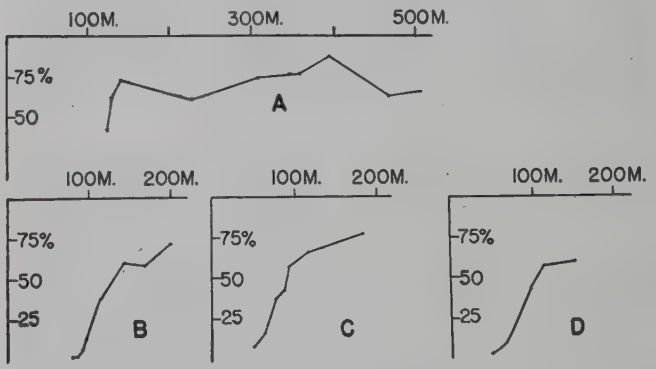

Figure 4. Relative abundance of planktonic Foraminifera in relation to depth.
A. Marthas Vineyard traverse
B. Block Island traverse
C. New Jersey traverse
D. Maryland traverse

PLANKTONIC FORAMINIFERA

The planktonic Foraminifera are confined almost entirely to the area south of Cape Cod. They appear in the four deepest samples of the Cape Cod Light traverse where they form 2.6% of the fauna at 121 meters increasing to 19.6% at 144 meters and decreasing again to 11.3% at 203 meters. At the latter station the actual abundance is almost three times that of the 144 meter station. The planktonic fauna in these samples is composed almost entirely of *Globigerina eggeri* v. Rhumbler. The only other occurrence of planktonic forms in the

northern area is in the shallowest sample of this traverse at a depth of ½ meter. This is the sample which was mentioned earlier as containing an alien fauna probably brought from the south by longshore currents. All the planktonic specimens in this traverse were much smaller than the normal adult specimens of the southern area. No planktonic Foraminifera were found in the Ipswich Bay traverse.

A study of the curves plotted to show the relative proportions of planktonic to benthonic specimens in the area south of Cape Cod shows that in water of less than 50 meters in depth the planktonic forms are practically negligible. It should be said here that this method of measuring the relative abundance of the planktonic forms has flaws due to the fluctuations of the benthonic fauna. It was found, however, as has been mentioned previously, that the total abundance of the planktonic forms varied between samples very much as did the benthonic. A study of the tables listing the planktonic fauna will reveal these fluctuations in the abundance, and a comparison may be made with those of the benthonic forms. For this reason the representation on the chart of the relative percentages of the planktonic to benthonic forms seems to be the most trustworthy method of presenting the facts. The introduction of depth also, is, in itself, irrelevant, but as a means of fixing the areal limits of the organisms it is useful. From the 50 meter point outward there is a rapid increase in the relative percentage of planktonic forms until at the break in slope, or slightly deeper, they form as high as 80% of the Foraminifera found. In the Marthas Vineyard traverse, which extends farther out onto the slope than the others, the percentages dropped somewhat in the two deepest samples after reaching a maximum of 80% at 393 meters. This may show that this is the inner limit of the environment that is favorable for the planktonic fauna found in the western North Atlantic. A continued increase outward, on the other hand, would show that conditions were still on the border line, being favorable, perhaps, only at certain times of year.

In the southern region there are fifteen species which are present in sufficient quantities to be given a percentage rating. Of these, three species of *Globigerina* form the bulk. They are, in order of importance: *Globigerina eggeri* Rhumbler, *Globigerina bulloides* d'Orbigny, and *Globigerina inflata* d'Orbigny. It is possible that the forms included under the name *Globigerina eggeri* are of more than one species. Many of the specimens are very small but they closely resemble the large, well-developed form that may definitely be assigned to that species. *Globigerina inflata* maintains a fairly constant percentage of the samples but *Globigerina eggeri* increases somewhat with distance from

the shore while *Globigerina bulloides* decreases. The remaining twelve species are present in very small relative quantities and are very spotty in occurrence. It is interesting to note that the specimens of *Globigerinoides rubra* (d'Orbigny) found lack the rosy color typical of those occurring south of Cape Hatteras.

Sir John Murray in a discussion of planktonic Foraminifera (1897) says that on the *Challenger* expedition the dead tests were never found at the bottom when the living forms were absent from the plankton. For this reason he believed that the rate of fall to the bottom after death was rapid. He accounts for the disappearance of the planktonic forms at the edge of the continental shelf on the basis of changing temperature conditions. It seems equally probable that salinity change may play an important part. In the coastal waters the salinity is lowest on the surface and increases with depth, while the reverse is true in deep water. In addition, the relatively fresh coastal waters are at most times less dense than the corresponding layer offshore so that a current is maintained which tends to have its greatest strength just outside the 100 fathom curve (Iselin, 1939). Small scale mixing processes at this point result in a rapidly changing temperature-salinity correlation across the boundary. It is across this boundary also that the relative abundance of planktonic Foraminifera decreases rapidly shoreward. Whether this decrease is due to the physical characteristics of the water or to the mechanical difficulty of the transportation of the forms nearer shore is open to question.

CONCLUSIONS

(1) Evidence of four definite faunal zones running parallel to the coast from Cape Cod to Maryland has been found. Definite zones east and north of Cape Cod could not be established due probably to the complete mixing of the water in winter, lower temperatures throughout the year, and the great annual variation of temperature.

(2) An analysis of the various physical conditions points to the probability that temperature is the chief controlling factor in the distribution of the Foraminifera in this area. Light, salinity, and food supply probably exert control also.

(3) No reason for the varying abundance of the Foraminifera was found, though the abundance increases to some extent with depth. Mechanical agencies such as differential rate of sedimentation or transportation of the tests may cause localized differences in abundance.

(4) The planktonic fauna is confined almost entirely to the region south of Cape Cod, with the greatest abundance at about 400 meters. Temperature and salinity changes appear to be the main factors which cause the disappearance of the planktonic Foraminifera shoreward from this point.

SPECIES REFERRED TO IN TEXT AND TABLES

Ammodiscus sp. (Pl. 1, fig. 6)
Ammosphaeroidina sphaeroidiniformis (H. B. Brady) (Pl. 4, fig. 3)
Angulogerina angulosa (Williamson) (Pl. 5, fig. 21)
Angulogerina angulosa (Williamson) var. (Pl. 4, fig. 12)
Angulogerina sp. 1. (Pl. 1, fig. 14)
Angulogerina sp. 2. (Pl. 5, fig. 22)
Astrononion stellatum Cushman and Edwards (Pl. 5, fig. 6)

Bolivina pseudoplicata Heron-Allen and Earland (Pl. 1, fig. 13)
Bolivina subaenariensis Cushman (Pl. 5, fig. 17)
Bolivina subspinescens Cushman (Pl. 4, fig. 8)
Bolivina sp. 1. (Pl. 5, fig. 16)
Bolivina sp. 2. (Pl. 5, fig. 18)
Bulimina aculeata d'Orbigny (Pl. 5, fig. 12)
Bulimina (*Desinobulimina*) *auriculata* Bailey (Pl. 5, fig. 9)
Bulimina exilis (H. B. Brady) (Pl. 4, fig. 9)
Bulimina marginata d'Orbigny (Pl. 5, fig. 11)
Bulimina marginata d'Orbigny var. (Pl. 4, fig. 10)
Bulimina (*Desinobulimina*) *turgida* Bailey (Pl. 5, fig. 10)
Bulimina sp. (Pl. 5, fig. 13)
Buliminella elegantissima (d'Orbigny) (not figured)

Cancris sagra (d'Orbigny) (Pl. 3, figs. 11 a, b)
Cassidulina crassa d'Orbigny (Pl. 6, figs. 5 a, b)
Cassidulina laevigata d'Orbigny (Pl. 6, fig. 4)
Cassidulina norcrossi Cushman (Pl. 6, figs. 2 a, b)
Cassidulina subglobosa H. B. Brady (Pl. 6, figs. 3 a, b)
Cassidulina sp. (Pl. 6, figs. 6 a, b)
Cassidulinoides bradyi (Norman) (Pl. 3, fig. 12)
Chilostomella ovoidea Reuss (Pl. 3, fig. 15)
Cibicides concentrica (Cushman) (Pl. 1, figs. 16 a, b)
Cibicides pseudoungeriana (Cushman) (Pl. 6, figs. 7 a, b)
Cibicides refulgens (Montfort) (Pl. 6, figs. 10 a, b) [1]

Dentalina advena (Cushman) (not figured)
Dentalina filiformis (d'Orbigny) (not figured)
Dentalina mucronata (Neugeboren) (Pl. 5, fig. 1)

[1] *Cibicides lobatulus* (Walker and Jacob) is included with this species.

Discorbis bertheloti (d'Orbigny) (Pl. 3, figs. 5 a, b)
Discorbis floridana Cushman (Pl. 5, figs. 23 a, b)
Discorbis obtusa d'Orbigny (Pl. 5, figs. 24 a, b)
Discorbis sp. 1. (not figured)
Discorbis sp. 2. (Pl. 1, fig. 15)
Discorbis sp. 3. (not figured)

Eggerella advena Cushman (Pl. 1, fig. 2)
Elphidium incertum (Williamson) (Pl. 5, fig. 7)
Elphidium subarcticum Cashman (Pl. 5, fig. 4)
Elphidium sp. (Pl. 1, fig. 12)
Entosolenia (several species, not figured)
Epistomina elegans (d'Orbigny) (Pl. 3, fig. 9)
Eponides frigida (Cushman) var. *calida* Cushman and Cole (Pl. 5, figs. 25 a, b)
Eponides umbonata (Reuss) (Pl. 6, figs. 1 a, b)
Eponides umbonata (Reuss) var. *ehrenbergi* (Bailey) (Pl. 3, figs. 16 a, b)
Eponides sp. (Pl. 3, figs. 13 a, b)

Gaudryina (*Pseudogaudryina*) *atlantica* (Bailey) (Pl. 2, fig. 3)
Globigerina bulloides d'Orbigny (Pl. 7, figs. 1, 2)
Globigerina eggeri Rhumbler (Pl. 7, figs. 5, 6)
Globigerina inflata d'Orbigny (Pl. 6, figs. 12, 13)
Globigerinella aequilateralis (H. B. Brady) (Rare — planktonic, not figured)
Globigerinoides conglobata (H. B. Brady) (Pl. 7, figs. 8, 9)
Globigerinoides rubra (d'Orbigny) (Pl. 7, fig. 4)
Globigerinoides sacculifera (H. B. Brady) (Pl. 7, fig. 7)
Globorotalia hirsuta (d'Orbigny) (Pl. 7, figs. 11, 14)
Globorotalia menardii (d'Orbigny) (Pl. 7, fig. 10)
Globorotalia truncatulinoides (d'Orbigny) (Pl. 7, figs. 12, 15)
Globorotalia tumida (H. B. Brady) (Pl. 7, figs. 16, 17)
Globulina inaequalis Reuss (Pl. 1, fig. 8)
Globulina inaequalis Reuss var. *caribaea* d'Orbigny (Pl. 1, fig. 10)
Guttulina lactea (Walker and Jacob) (Pl. 5, fig. 3)
Guttulina sp. (not figured)
Gyroidina orbicularis d'Orbigny (Pl. 4, figs. 14 a, b)
Gyroidina soldanii d'Orbigny (Pl. 3, figs. 8 a, b)

Haplophragmoides columbiensis Cushman (Pl. 4, fig. 17)
Haplophragmoides glomeratum (H. B. Brady) (Pl. 4, fig. 16)
Haplophragmoides major Cushman (Pl. 1, fig. 1)
Haplophragmoides subglobosum (G. O. Sars) (Pl. 4, fig. 18)
Haplophragmoides sp. (Pl. 4, fig. 20)

Karreriella affinis (Fornasini) (Pl. 2, fig. 7)
Karreriella bradyi (Cushman) (Pl. 4, fig. 5)
Karreriella (?) sp. (not figured)

Lagena hexagona (Williamson) (Pl. 4, fig. 19)
Lagena laevis (Montagu) var. *nebulosa* Cushman (Pl. 4, fig. 24)
Lagena torquata H. B. Brady (Pl. 4, fig. 23)
Lenticulina peregrina (Schwager) (Pl. 4, fig. 25)
Listerella nodulosa (Cushman) (Pl. 4, fig. 4)

Marginulina bacheii Bailey (Pl. 3, fig. 1)
Massilina sp. (Pl. 2, fig. 8)

Nodosaria pyrula d'Orbigny (Pl. 5, fig. 2)
Nonion cf. *barleeanum* (Williamson) (Pl. 3, fig. 3)
Nonion grateloupi (d'Orbigny) (Pl. 3, fig. 4)
Nonion grateloupi (d'Orbigny) var. (Pl. 4, fig. 7)
Nonion labradoricum (Dawson) (Pl. 5, fig. 5)
Nonion sloanii (d'Orbigny) (Pl. 1, fig. 11)
Nonionella turgida (Williamson) (Pl. 3, figs. 6 a, b)

Orbulina universa d'Orbigny (Pl. 6, fig. 11)

Planulina foveolata (H. B. Brady) (Pl. 3, figs. 17 a, b)
Planulina mera Cushman (Pl. 6, figs. 9 a, b)
Plectina apicularis (Cushman) (Pl. 2, fig. 6)
Poroeponides lateralis (Terquem) (Pl. 1, figs. 17 a, b)
Proteonina difflugiformis (H. B. Brady) (Pl. 4, fig. 15)
Pseudoclavulina novangliae (Cushman) (Pl. 2, fig. 14)
Pseudoglandulina occidentalis (Cushman) (Pl. 4, fig. 6)
Pseudopolymorphina atlantica Cushman and Ozawa (Pl. 3, fig. 2)
Pullenia quinqueloba (Reuss) (Pl. 6, fig. 8)
Pulleniatina obliquiloculata (Parker and Jones) (Pl. 7, fig. 13)
Pulvinulinella cf. *exigua* (H. B. Brady) (Pl. 3, fig. 14)
Pyrgo cf. *denticulata* (H. B. Brady) (Pl. 2, fig. 9)
Pyrgo elongata (d'Orbigny) (not figured)
Pyrgo striatella (Cushman) (Pl. 1, fig. 9)
Pyrgo subsphaerica (d'Orbigny) (Pl. 2, fig. 10)

Quinqueloculina seminulum (Linnaeus) (Pl. 1, figs. 3 a, b)
Quinqueloculina seminulum (Linnaeus) var. *jugosa* Cushman (Pl. 1, fig. 5)

Robertina arctica d'Orbigny (Pl. 5, fig. 8)
Robertina sp. (Pl. 3, fig. 7)
Robulus sp. 1. (Pl. 2, fig. 12)
Robulus sp. 2. (Pl. 2, fig. 13)
Robulus sp. 3. (Pl. 2, fig. 11)

Sigmoilina schlumbergeri Silvestri (not figured)
Sphaeroidina bulloides d'Orbigny (Pl. 7, fig. 3)
Sphaeroidinella dehiscens (Parker and Jones) (rare planktonic, not figured)
Spiroplectammina sp. (Pl. 4, fig. 21)

Textularia candeiana d'Orbigny (Pl. 2, fig. 5)
Textularia goessi Cushman (?) (Pl. 2, fig. 1)
Textularia pseudotrochus Cushman (Pl. 2, fig. 2)
Triloculina tricarinata d'Orbigny (not figured)
Triloculina sp. (Pl. 1, figs. 4 a, b)
Trochammina globigeriniformis (Parker and Jones) (Pl. 2, fig. 4)
Trochammina globulosa Cushman (Pl. 4, figs. 22 a, b)
Trochammina lobata Cushman (Pl. 1, figs. 7 a, b)
Trochammina ochracea (Williamson) (not figured)
Trochammina sp. (not figured)

Uvigerina peregrina Cushman (Pl. 4, fig. 11)
Uvigerina peregrina Cushman var. *bradyana* Cushman (Pl. 5, fig. 20)
Uvigerina sp. (Pl. 5, fig. 19)

Valvulina conica Parker and Jones (Pl. 4, figs. 1, 2)
Valvulineria sp. (Pl. 4, figs. 13 a, b)
Virgulina compressa (Bailey) (Pl. 3, fig. 10)
Virgulina fusiformis Williamson (Pl. 5, fig. 15)
Virgulina sp. (Pl. 5, fig. 14)

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TABLE 1. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE MARYLAND TRAVERSE

Atlantis Station	1236a	1236d	1237b	1237d	1237f	1238a	1238c	1238e	1238h	1239a	1239c	1239d	1239e	1239f	1240a
Position	38° 12′ N 75° 02′ W	—	—	—	—	38° 02′ N 74° 37′ W	—	—	—	37° 55′ N 74° 20′ W	—	—	—	—	37° 49′ N 74° 07′ W
Distance from starting point (nautical miles)	—	5.7	11.4	15.2	19	22.6	26.0	29.4	34.5	36.5	40.5	42.5	44.5	46.5	
Depth (meters)	22	24.5	32	22	35	37	44	52	63	68	77	99	114	154	386
Proteonina difflugiformis			0.9		2.5	4.7	2.7	1.7	2.2	3.1	1.9	0.5	0.5		
Pseudoclavulina novangliae														0.1	
Eggerella advena		0.5			7.7			1.7	0.8	0.8	0.6	0.3			
Listerella nodulosa															1.9
Quinqueloculina seminulum	6.3	2.9	2.9	4.7	13.6	3.4	15.3	1.0							
Quinqueloculina seminulum var. jugosa			0.8	1.6											
Massilina sp.													0.5	0.1	
Triloculina sp.								1.5	1.2	1.3	1.1	0.6	0.2		
Pyrgo elongata													0.2		
Pyrgo striatella									0.3	0.2	0.2				
Pyrgo cf. denticulata												0.4			
Trochammina lobata	0.6	0.7	1.2				1.6	0.4	0.3	0.3					
Robulus sp. 2										0.4	0.7	1.3	0.7	3.3	
Robulus sp. 3												0.3		0.4	
Marginulina bacheii										0.1	0.7	2.5	1.1	0.4	
Nodosaria pyrula														0.1	
Lagena hexagona													0.2	0.3	
Lagena laevis var. nebulosa														0.1	
Miscellaneous Lagena												0.3	0.3	0.3	
Miscellaneous Lagenidae									0.8	0.5	0.7	0.7	0.7	0.7	1.1
Globulina inaequalis									0.6	0.2					
Globulina inaequalis var. caribaea						2.0	2.2	0.6	0.3	0.4	0.4	0.2			
Guttulina lactea			2.4		2.0	1.4	1.6	1.5	2.6	2.2	1.1	0.9	0.3	0.2	
Nonion sloanii								0.4	0.2						
Nonion cf. barleeanum												0.2	0.3	0.1	
Nonion labradoricum													0.2	0.1	
Nonion grateloupi													0.1	0.3	
Nonionella turgida													0.3	0.2	
Elphidium incertum	77.6	65.4	68.6	65.6	39.9	31.1	28.6	37.5	29.3	21.5	12.5	9.7	8.1	5.8	18.2
Elphidium sp.	5.0	9.6	4.8	3.1	2.2										
Elphidium subareticum	3.3	1.8	3.6	4.7	4.7	3.4	7.7	22.2	22.6	22.8	19.1	13.2	6.0	0.5	1.2
Buliminella elegantissima		1.8													
Bulimina (Desinobulimina) turgida														0.2	
Bulimina (Desinobulimina) auriculata														0.3	
Bulimina marginata		0.3				4.1		0.3	2.2	2.5	7.4	16.7	23.1	21.9	39.3
Bulimina marginata var.															0.4
Bulimina sp.									0.3	0.3	0.4	0.2	0.4		

Atlantis Station	1236a	1236d	1237b	1237d	1237f	1238a	1238c	1238e	1238h	1239a	1239c	1239d	1239e	1239f	1240a
Position	38° 12′ N 75° 02′ W	—	—	—	—	38° 02′ N 74° 37′ W	—	—	—	37° 55′ N 74° 20′ W	—	—	—	—	37° 49′ N 74° 07′ W
Distance from starting point (nautical miles)	—	5.7	11.4	15.2	19	22.6	26.0	29.4	34.5	36.5	40.5	42.5	44.5	46.5	
Depth (meters)	22	24.5	32	22	35	37	44	52	63	68	77	99	114	154	386
Virgulina fusiformis		0.8			1.5			2.4		0.2	0.5	1.0	2.0	5.5	
Virgulina sp.						6.1				0.3	0.2	0.9	1.1	1.3	0.4
Virgulina compressa													0.1	0.6	
Bolivina sp. 1		0.9				2.7				0.2	0.1	0.6	2.3	13.0	6.2
Bolivina pseudoplicata		0.8			2.2	4.1		1.3	0.6	0.7	0.3	0.4	0.5	0.4	
Bolivina sp. 2														0.4	
Bolivina subaenariensis													0.2	1.4	0.2
Uvigerina sp.													0.1	4.1	1.8
Uvigerina peregrina var. bradyana												0.2	0.3	0.9	1.0
Angulogerina angulosa									0.7	0.8	1.7	5.5	8.1	7.1	10.3
Entosolenia												0.1	0.5	0.4	
Discorbis sp. 2		1.6	1.2												
Discorbis floridana		4.3	0.5		2.7			0.2	0.2	0.4	0.8	0.9	1.3	0.3	
Discorbis obtusa								0.4	0.2	0.2		0.3			
Gyroidina orbicularis															0.1
Epondes frigida var. calida	1.3	0.7	0.5					0.6	0.5	0.5	0.1	1.2	1.6	0.6	1.5
Eponides sp.													0.5	0.6	
Eponides umbonata														0.2	0.4
Cancris sagra												0.1			
Pulvinulinella cf. exigua												0.7	1.5	1.0	
Epistomina elegans												0.2	0.2	1.0	
Cassidulina subgobosa						6.7		0.4	0.6	1.0	5.7	10.6	11.6	5.3	5.7
Cassidulina norcrossi												0.4	1.1	1.9	6.2
Cassidulina laevigata												1.5	2.7	4.2	1.7
Cassidulina sp.												0.5	0.6	1.7	0.4
Cassidulina crassa													1.0	2.0	0.4
Cassidulinoides bradyi														0.6	
Pullenia quinqueloba														0.3	
Cibicides concentrica	2.1	2.6	3.6	3.1	2.0	4.1	16.5	2.9	0.6	0.2					
Planulina mera		0.6	3.8	6.3	5.4	4.7	9.9	4.5	0.8	0.7	1.0	1.2	1.1	1.2	
Cibicides pseudoungeriana									0.8	1.8	3.1	7.1	8.1	4.2	0.2
Cibicides refulgens	0.9				1.5	6.1	6.6	17.4	30.6	35.8	38.6	17.3	7.9	2.7	0.6
Planulina foveolata												0.2	0.8	0.8	
Miscellaneous	2.9	4.8	5.1	10.9	12.1	15.5	7.1	1.2	0.8	0.8	1.0	1.2	1.7	0.9	0.7
Estimated number of specimens	850	1350	600	75	400	150	200	6100	13500	17250	11700	63200	58800	425700	106000

TABLE 2. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE NEW JERSEY TRAVERSE

Atlantis Station	1245a	1244c	1244a	1243f	1243d	1243b	1242f	1242d	1242c	1242b	1242a	1241c	1241b
Position	39° 14′ N 73° 54′ W	—	39° 07′ N 73° 43′ W	—	—	—	—	—	—	—	38° 47′ N 73° 06′ W	—	—
Distance from starting point (nautical miles)	—	5.4	10.7	15.9	21.1	26.3	32.3	38.3	41.3	44.3	46.7	49.1	51.5
Depth (meters)	45.5	36	43	53	53	66	74	77	82	90	117.7	182	610
Proteonina difflugiformis	20.5	10.4	4.8	6.1	4.9	7.2	2.9						2.9
Pseudoclavulina novangliae											0.4	0.5	
Gaudryina (Pseudogaudryina) atlantica												0.8	
Eggerella advena	6.7	12.4		3.8	3.6	6.8	1.8						
Listerella nodulosa													2.3
Valvulina conica													0.7
Quinqueloculina seminulum	1.2	11.9	11.1										
Massilina sp.											0.5		
Triloculina sp.	1.7	1.0	4.8		2.8	1.1	0.6	0.6					
Trochammina lobata	1.9			0.6		0.7							
Robulus sp. 1											0.3	0.6	
Robulus sp. 2										1.2	1.3	1.5	
Marginulina bacheii											1.5	0.8	
Dentalina advena											0.1		
Dentalina mucronata												0.3	
Dentalina filiformis												0.1	
Miscellaneous Lagena												0.8	
Miscellaneous Lagenidae								1.4	1.6	5.1	1.5	2.0	1.7
Globulina inaequalis			1.6										
Globulina inaequalis var. caribaea		1.0	4.8										
Guttulina lactea	2.6	3.6	20.6	0.7		1.7	0.6			1.5	0.2		
Nonion labradoricum													0.8
Nonion grateloupi											0.3		
Nonionella turgida											0.2		
Elphidium incertum	40.4	30.1	17.5	48.2	11.3	13.9	26.1	3.8	2.7	0.6	0.4	1.5	11.4
Elphidium subarcticum	12.0	5.2	7.9	5.3	4.9	11.3	5.3	3.8	13.0	9.8	0.4		
Bulimina marginata						1.0	18.8	17.4	20.4	10.7	11.6	7.8	11.1
Bulimina marginata var.													10.6
Bulimina (Desinobulimina) turgida											0.3	0.9	2.0
Bulimina exilis													4.4
Virgulina fusiformis	1.4			0.6				1.8	1.5	1.4	2.4	0.7	1.1
Virgulina sp.							1.0						2.3

Atlantis Station	1245a	1244c	1244a	1243f	1243d	1243b	1242f	1242d	1242c	1242b	1242a	1241c	1241b
Position	39° 14′ N 73° 54′ W	—	39° 07′ N 73° 43′ W	—	—	—	—	—	—	—	38° 47′ N 73° 06′ W	—	—
Distance from starting point (nautical miles)	—	5.4	10.7	15.9	21.1	26.3	32.3	38.3	41.3	44.3	46.7	49.1	51.5
Depth (meters)	45.5	36	43	53	53	66	74	77	82	90	117.7	182	610
Virgulina compressa											0.2	0.8	
Bolivina sp. 1	0.6	7.8						0.7	1.1		2.9	6.5	12.8
Bolivina pseudoplicata	2.0	2.1		1.5									
Bolivina subaenariensis											0.4	0.6	0.9
Uvigerina sp.											0.7	1.0	0.9
Uvigerina peregrina var. bradyana											0.9	0.8	0.5
Angulogerina sp. 1	0.3												
Angulogerina angulosa							1.7	4.5	7.1	9.1	24.7	7.5	1.0
Angulogerina angulosa var.													0.4
Discorbis floridana								0.7		1.8	0.9		
Gyroidina soldanii												1.7	
Gyroidina orbicularis													0.2
Eponides frigida var. calida	1.5	1.0		0.6			2.6						
Eponides umbonata var. ehrenbergi												0.5	
Valvulineria sp.													1.1
Epistomina elegans											2.0	2.3	
Cassidulina subglobosa		1.6					2.1	14.6	14.8	9.4	8.5	7.8	2.0
Cassidulina norcrossi							0.2				1.2		14.3
Cassidulina laevigata								1.3	1.1		3.2	9.9	3.2
Cassidulina sp.											1.9	8.1	
Cassidulina crassa											5.4	10.1	1.1
Cassidulinoides bradyi												0.5	
Pullenia quinqueloba													1.3
Cibicides pseudoungeriana							1.5	5.0	6.8	21.6	17.5	11.5	1.7
Cibicides refulgens	2.0	7.3	27.0	31.2	67.8	54.1	31.8	39.0	24.7	20.3	2.8	4.8	1.9
Cibicides concentrica	2.6	1.0											
Planulina mera	1.1												
Planulina foveolata											1.9	2.8	
Miscellaneous	1.6	3.6		1.6	4.9	2.3	2.9	5.2	5.3	7.5	3.5	4.3	5.5
Estimated number of specimens	2300	200	100	11300	700	5900	14900	4900	3100	4400	140500	107000	5800

TABLE 3. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE BLOCK ISLAND TRAVERSE

Sample	2	5	9	13	15	21	25	31	36	39	43	46	49	49a	50	52
Distance from starting point (miles)	1	4	8⅛	13⅜	21	29⅜	34⅛	41	47⅛	50⅜	55⅛	59	62	63	65	67
Depth (meters)	19	43	43	55	67½	71	70	81	80	85	93	97	112	142	167	200
Proteonina difflugiformis		25.1	3.2	15.9	60.6	78.7	60.4	47.6	17.0	9.3	0.5					
Haplophragmoides major					0.8	0.9		0.8								
Textularia goessi (?)											0.3	0.4	0.1			
Gaudryina (Pseudogaudryina) atlantica												0.4	1.6	2.0	1.2	4.0
Pseudoclavulina novangliae											1.0	2.5	4.6	2.1	2.0	2.2
Eggerella advena		21.4	16.0	57.2	14.7	4.9	3.9	6.5	2.4							
Plectina apicularis											0.3					
Quinqueloculina seminulum	7.5	4.5	5.3									0.2		0.1		
Massilina sp.																
Triloculina sp.		5.9	9.6									0.2				
Pyrgo cf. denticulata																
Trochammina lobata				1.4								0.4	0.9	0.4	1.0	1.9
Robulus sp. 1									0.6	0.5	1.4	1.6	5.8	1.2	0.9	1.9
Robulus sp. 2															0.5	0.4
Robulus sp. 3											2.0	6.6	11.6	1.6	0.8	0.6
Marginulina bacheii														0.1	0.1	0.2
Lenticulina peregrina													0.4	0.1	0.3	0.7
Dentalina mucronata									1.0	0.7	0.3	1.0	1.4	1.6	0.9	2.0
Misc. Lagenidae													0.5			
Guttulina lactea		3.7	5.3													
Globulina inaequalis var. caribaea			4.3										0.2	0.4	0.2	
Nonion cf. barleeanum													0.2	0.2	0.1	
Nonion labradoricum														0.1	0.1	
Nonion grateloupi												0.3	0.2	0.3	0.3	0.3
Nonionella turgida		16.3	25.3	12.2	12.7	10.4	23.1	30.0	39.7	47.0	22.4	5.1	0.5	1.3	0.5	1.5
Elphidium incertum															0.4	
Elphidium subarcticum	0.8	10.0	9.6	0.3												
Bulimina aculeata	2.0										0.6	1.4	3.2	2.8	1.6	3.4
Bulimina (Desinobulimina) turgida								1.0	7.6	7.3	2.3	0.6	0.3			
Bulimina (Desinobulimina) auriculata																

Sample	2	5	9	13	15	21	25	31	36	39	43	46	49	49a	50	52
Distance from starting point (miles)	1	4	8⅛	13⅜	21	29⅜	34⅛	41	47⅛	50⅜	55⅛	59	62	63	65	67
Depth (meters)	19	43	43	55	67½	71	70	81	80	85	93	97	112	142	167	200
Bulimina marginata			2.1		0.8	1.0	3.8	1.8	14.9	18.0	52.4	62.0	35.0	27.0	21.8	11.2
Virgulina compressa												0.4	0.4	1.8	3.0	1.3
Virgulina fusiformis									0.4	0.5	0.4	0.7		0.4	0.3	0.2
Virgulina sp.					1.1			1.0	0.5	0.3		0.4				
Bolivina pseudoplicata		1.5	2.1													
Bolivina sp. 1												1.3	0.7	2.3	3.6	3.2
Uvigerina sp.													0.8	0.9	0.4	
Uvigerina peregrina var. bradyana										0.9	2.3	3.1	7.1	2.7	1.5	0.2
Angulogerina angulosa							0.8	0.7	1.0	0.5	1.3	3.4	5.6	14.9	13.3	26.7
Discorbis floridana	5.3	1.5														
Discorbis bertheloti														1.4	1.2	2.5
Poroeponides lateralis	80.0															
Gyroidina soldanii													0.3	1.4	2.2	4.4
Eponides frigida var. calida		2.2	9.6	10.8	7.7	2.2	6.1	8.0	9.3	9.8	5.7	1.9				
Eponides umbonata											0.2		0.3	0.2	0.4	0.2
Eponides umbonata var. ehrenbergi													0.4	0.4	1.3	2.3
Epistomina elegans													1.0	0.5	0.3	1.7
Cassidulina subglobosa								0.9				0.4	3.0	3.9	5.0	1.1
Cassidulina norcrossi									1.7	2.7	3.9	2.2	1.3	1.4	3.3	0.6
Cassidulina laevigata													0.7	6.7	9.7	3.4
Cassidulina sp.													2.1	0.3	0.3	0.5
Cassidulinoides bradyi														0.4	0.4	1.2
Cibicides pseudoungeriana											0.3	1.1	6.6	14.0	15.3	13.7
Cibicides refulgens		6.3											1.3	2.5	3.5	2.8
Panulina mera														0.3	0.3	0.2
Planulina foveolata													0.5	1.4	0.9	1.5
Miscellaneous	4.5	1.5	7.5	2.1	1.7	1.3	1.8	1.4	3.8	2.3	2.4	2.4	0.8	0.8	1.3	1.7
Estimated number of specimens	350	300	100	1100	650	900	800	1000	2500	2900	14350	16550	64600	120000	119500	74750

TABLE 4. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE MARTHAS VINEYARD TRAVERSE

Sample	1	2	3	4	5	6	7	8	9
Position	40° 10′ N 70° 48′ W	40° 07′ N 70° 48′ W	40° 06′ N 70° 48′ W	40° 03′ N 70° 48′ W	40° 01′ N 70° 48′ W	40° 00′ N 70° 48′ W	39° 59′ N 70° 48′ W	39° 58′ N 70° 48′ W	39° 57′ N 70° 48′ W
Depth (Meters)	122	128	140	228	309	359	393	469	680
Proteonina difflugiformis								5.0	
Textularia goessi(?)				0.1					
Gaudryina (Pseudogaudryina) atlantica	1.5	3.0	2.5	0.3					
Ammosphaeroidina sphaeroidiniformis									0.5
Pseudoclavulina novangliae	3.4	3.4	3.1	0.5					
Listerella nodulosa				0.6	4.5	2.1	12.6	25.3	1.9
Massilina sp.		0.2	0.6						
Robulus sp. 2	0.7	1.1	0.6	0.5					
Robulus sp. 3	2.4	1.7	0.7	0.7					
Lenticulina peregrina					0.2				
Marginulina bacheii	1.4	1.5	0.7						
Dentalina mucronata	0.4	0.2		0.4					
Lagena									0.9
Misc. Lagenidae	0.6	1.7	1.7	1.5	0.8	1.4	2.9		
Nonion cf. barleeanum	0.5	1.0	0.6						
Nonion labradoricum					0.5	1.0	1.8		1.0
Nonion grateloupi var.									0.3
Nonionella turgida		0.2		0.3					
Elphidium incertum	0.5			5.4	33.0	32.8	21.4	14.6	8.6
Bulimina aculeata							1.6	3.5	2.9
Bulimina (Desinobulimina) turgida	0.5	1.6	0.7	0.4		1.2	1.6		0.4
Bulimina (Desinobulimina) auriculata						0.8			
Bulimina marginata	28.5	32.5	9.2	13.1	2.5	2.2			
Bulimina marginata var.						2.2	6.0	17.4	49.7
Bulimina exilis						0.7	3.2	1.4	1.1
Virgulina compressa	0.7	1.2	0.7	0.9					
Virgulina fusiformis				0.3	0.3				1.1
Virgulina sp.					0.6	0.7			

Sample	1	2	3	4	5	6	7	8	9
Position	40° 10′ N 70° 48′ W	40° 07′ N 70° 48′ W	40° 06′ N 70° 48′ W	40° 03′ N 70° 48′ W	40° 01′ N 70° 48′ W	40° 00′ N 70° 48′ W	39° 59′ N 70° 48′ W	39° 58′ N 70° 48′ W	39° 57′ N 70° 48′ W
Depth (Meters)	122	128	140	228	309	359	393	469	680
Bolivina sp. 1	0.6	2.7	10.1	21.2	19.2	3.9	4.1	1.9	6.1
Bolivina subaenariensis					0.8	0.4			
Uvigerina sp.	0.3	1.4	1.0	0.2					
Uvigerina peregrina									1.6
Uvigerina peregrina var. bradyana	4.1	7.0	0.8	0.3					
Angulogerina angulosa	12.0	10.0	20.1	21.0	6.1	3.7	1.7		
Angulogerina angulosa var.									1.6
Discorbis bertheloti	0.5	1.1		0.5					
Discorbis floridana			1.0						
Gyroidina soldanii	0.5	2.0	1.9	2.9					
Gyroidina orbicularis					1.0	2.1	3.4	1.5	1.4
Eponides frigida var. calida				0.8	2.7	1.0	1.4		
Eponides umbonata	0.2	0.3		0.3	0.5		1.1		
Eponides umbonata var. ehrenbergi	0.5	1.5		0.5					
Eponides sp.			1.9						
Epistomina elegans	0.3	0.5	1.0	0.3					
Valvulineria sp.									1.8
Cassidulina subglobosa	8.9	1.8	2.9	0.9	3.9	8.7	4.3		
Cassidulina norcrossi	1.6	0.7	3.3	3.3	11.2	23.4	13.5	17.7	8.3
Cassidulina laevigata	7.5	1.7	5.0	9.6	4.9	1.2	0.8		1.6
Cassidulinoides bradyi			0.3	0.3	0.8				
Pullenia quinqueloba									0.4
Cibicides pseudoungeriana	15.0	15.2	10.0	8.2	3.4	1.8			
Cibicides refulgens	4.9	1.6	8.8	1.0	1.2	5.1	12.8	2.1	2.4
Planulina foveolata	0.8	1.8	3.1	0.3					
Miscellaneous	1.0	1.9	6.8	3.7	1.7	3.8	6.3	9.5	6.8
Estimated number of specimens	46150	119050	9800	182200	29200	5650	2000	3800	33200

TABLE 5. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE CAPE COD LIGHT TRAVERSE

Sample	2	3	4	5	6	7	8	9	10	11	14
Distance from starting point (miles)	1	2	3	4	5	6	7	8	9	10	13
Depth (meters)	12	32	48	70	85	91	103	121	145	144	203
Proteonina difflugiformis		18.6	24.4	20.0	3.0	4.3	18.0	21.4	26.8	10.6	16.2
Haplophragmoides glomeratum					11.5	26.8	24.0	10.8	6.1	11.4	2.5
Haplophragmoides sp.					0.9		2.2		1.1	1.4	1.0
Haplophragmoides columbiensis						2.2	4.8	2.4			
Haplophragmoides major		4.2	8.7		0.8	1.3	0.9	6.7	1.4	1.3	
Valvulina conica						1.3	10.0	7.0	3.8	1.4	0.5
Eggerella advena	33.4	66.0	27.4	37.6	61.0	32.4	18.7	3.4			
Quinqueloculina seminulum	11.1		3.0								
Trochammina globulosa						1.2	5.7	3.1	1.3		
Trochammina lobata				6.0	1.2						
Trochammina ochracea	5.5										
Trochammina sp.	16.7										
Nonion labradoricum								2.3	5.1	3.9	5.0
Elphidium incertum											4.1
Astrononion stellatum			3.0	1.7	3.1	1.9	1.1	3.7	4.7	8.9	1.5
Elphidium sp.	5.5										
Elphidium subarcticum	5.5	5.1	9.6	6.4	1.7	1.1	2.3	3.7	2.1	1.4	
Robertina arctica								1.4			
Bulimina (Desinobulimina) auriculata									2.5	1.9	12.4
Bulimina aculeata & marginata var.									0.8	2.0	8.8
Virgulina fusiformis				1.6	1.5		1.0		0.9		
Virgulina sp.								1.4	2.5	2.1	0.6
Bolivina subaenariensis									2.3	1.5	29.8
Angulogerina sp. 2				1.0							0.6
Angulogerina angulosa					4.9						
Entosolenia								1.5			
Discorbis sp. 1	11.1										
Discorbis sp. 3	11.1										
Eponides frigida var. calida			1.6	4.0	1.6	1.3			1.5	1.2	3.9
Cassidulina subglobosa		2.6	13.5	6.2	3.0	4.1	3.1	11.6	14.0	16.9	3.5
Cassidulina norcrossi											0.8
Cassidulina laevigata			3.9	11.2	3.8						0.7
Cibicides refulgens						20.5	5.2	11.6	12.1	17.9	3.6
Miscellaneous		3.4	4.8	5.8	2.2	3.1	3.4	8.1	11.0	16.4	4.6
Estimated number of specimens	18	125	450	1400	3000	2200	2200	900	1500	1200	6200

TABLE 6. PERCENTAGE DISTRIBUTION OF THE BENTHONIC FORAMINIFERA IN THE IPSWICH BAY TRAVERSE

Sample	1	5	7	9	10	11
Distance from starting point (miles)	0	2 8/10	4 2/10	5 6/10	6 1/10	6 8/10
Depth (meters)	9	28	37	47	66	71
Proteonina difflugiformis		27.2	16.3	2.1	10.3	9.6
Ammodiscus sp.	0.8					
Haplophragmoides major			1.2	0.9	1.1	1.3
Haplophragmoides glomeratum					2.5	3.3
Haplophragmoides subglobosom						1.5
Spiroplectammina sp.					7.2	6.2
Eggerella advena	81.2	42.4	67.4	78.4	74.0	74.0
Karreriella (?) sp.						2.3
Sigmoilina schlumbergeri	1.6					
Trochammina globulosa	3.2					
Trochammina lobata	13.3	1.0	3.9	2.1	1.6	
Elphidium incertum		1.5	1.7			
Elphidium subarcticum		18.8	1.7	3.5		
Eponides frigida var. calida		4.6	1.1	3.5		
Cassidulina subglobosa		0.8	1.1	1.9		
Cibicides refulgens			2.2	3.8		
Miscellaneous		3.6	3.3	3.8	3.5	1.9
Estimated number of specimens	125	1500	200	450	725	700

TABLE 7. PERCENTAGE DISTRIBUTION OF THE PLANKTONIC FORAMINIFERA IN THE MARYLAND TRAVERSE

Atlantis Station	1238e	1238h	1239a	1239c	1239d	1239e	1239f	1240a
Position			37° 55′ N 74° 20′ W					37° 49′ N 74° 07′ W
Distance from starting point (nautical miles)	29.4	34.5	36.5	40.5	42.5	44.5	46.5	
Depth (meters)	52	63	68	77	99	114	154	386
Sphaeroidina bulloides					0.1	0.2	0.3	0.4
Globigerina bulloides	36.3	32.7	47.8	33.4	34.5	34.4	36.7	14.5
Globigerina eggeri	39.9	25.6	25.8	38.9	39.8	42.5	51.0	63.2
Globigerina inflata	10.4	20.5	14.9	19.6	16.9	18.2	10.3	19.4
Globigerinoides rubra	2.6	9.1	3.2	3.1	3.6	1.3	0.6	
Globigerinoides sacculifera	2.1	0.9	1.9	0.8	1.5	0.6	0.1⁻	0.3
Globigerinoides conglobata	6.2	5.6	2.9	3.0	1.9	1.2	0.4	0.7
Orbulina universa		0.9	0.3		0.5	0.2	0.1	
Pullenjatina obliquiloculata	2.1	0.5	0.7		0.3	0.2	0.1	
Globorotalia menardii	0.5	4.1	1.9	0.8	0.8	0.9	0.4	1.3
Globorotalia truncatulinoides						0.1	0.1⁻	
Globorotalia tumida								0.1
Miscellaneous			0.6	0.6	0.1			0.1⁻
Estimated number of specimens	200	800	18900	2700	46500	75000	636700	88700
Percentage of the planktonic Foraminifera to total fauna	3.1	5.2	8.5	18.7	42.4	56.0	59.9	45.5

TABLE 8. PERCENTAGE DISTRIBUTION OF THE PLANKTONIC FORAMINIFERA IN THE NEW JERSEY TRAVERSE

Alantis Station	1243d	1243b	1242f	1242d	1242c	1242b	1242a	1241c	1241b
Position							38° 47′ N 73° 06′ W		
Distance from starting point (nautical miles)	21.1	26.3	32.3	38.3	41.3	44.3	46.7	49.1	51.5
Depth (meters)	53	66	74	77	82	90	117.7	182	610
Sphaeroidina bulloides							0.7	1.7	0.4
Globigerina bulloides	45.8	58.8	37.7	34.5	27.1	21.1	29.2	42.2	9.7
Globigerina eggeri	22.9	19.7	45.7	46.5	57.7	45.2	47.1	29.1	72.3
Globigerina inflata	20.8	18.8	14.6	15.7	11.1	22.9	18.9	22.2	16.0
Globigerinoides rubra	4.2	1.4	0.8	1.4	1.7	3.1	1.1	1.3	0.1
Globigerinoides sacculifera				0.4		1.0	0.7	0.7	
Globigerinoides conglobata	2.1	0.6		1.2	1.2	4.7	0.8	0.9	0.4
Orbulina universa		0.3				0.3	0.3	0.8	0.1
Pulleniatina obliquiloculata						0.2	0.2	0.1⁻	0.1
Globorotalia menardii	2.1	0.4			0.4	1.6	0.9	0.8	0.9
Globorotalia truncatulinoides	2.1					0.1⁻		0.1	0.1⁻
Globorotalia tumida									0.1⁻
Miscellaneous			1.2	0.4	0.8				
Estimated number of specimens	50	700	3100	2800	2100	5700	295100	350500	13400
Percentage of the planktonic Foraminifera to total fauna	6.3	10.5	17.6	36.2	40.5	56.6	67.8	76.6	69.8

TABLE 9. PERCENTAGE DISTRIBUTION OF THE PLANKTONIC FORAMINIFERA IN THE BLOCK ISLAND TRAVERSE

Sample	36	39	43	46	49	49a	50	52
Distance from starting point (miles)	47 1/5	50 3/5	55 4/5	59	62	63	65	67
Depth (meters)	80	85	93	97	112	142	167	200
Sphaeroidina bulloides	2.4	3.7	13.9	15.4	10.2	5.2	8.0	7.6
Globigerina bulloides	78.0	18.8	12.8	18.9	14.1	25.8	28.0	27.6
Globigerina eggeri		59.1	53.4	47.7	57.6	51.7	51.5	36.1
Globigerina inflata	7.3	11.0	9.6	9.9	11.0	13.0	8.1	23.0
Globigerinoides rubra	7.3	0.9	2.6	1.7	0.8	1.1	1.6	1.7
Globigerinoides sacculifera		0.9	1.4	1.2	0.9	0.9	0.6	1.0
Globigerinoides conglobata	4.9	1.9	3.1	2.4	2.3	0.8	0.6	1.4
Orbulina universa		0.9	1.0	0.8	0.2	0.3	0.2	0.5
Pulleniatina obliquiloculata		0.9	0.9	0.5	0.3	0.3	0.3	0.2
Globorotalia menardii		0.9	1.1		1.5	0.9	0.8	0.7
Globorotalia hirsuta		0.9						
Globorotalia truncatulinoides					0.1			0.1
Miscellaneous				1.6			0.1	0.1
Estimated number of specimens	60	110	1000	2400	41900	186100	174100	185600
Percentage of the planktonic Foraminifera to total fauna	2.5	2.5	6.4	13.0	39.3	60.8	59.4	71.3

TABLE 10. PERCENTAGE DISTRIBUTION OF THE PLANKTONIC FORAMINIFERA IN THE MARTHAS VINEYARD TRAVERSE

Sample	1	2	3	4	5	6	7	8	9
Position	40° 10′ N 70° 48′ W	40° 07′ N 70° 48′ W	40° 06′ N 70° 48′ W	40° 03′ N 70° 48′ W	40° 01′ N 70° 48′ W	40° 00′ N 70° 48′ W	39° 59′ N 70° 48′ W	39° 58′ N 70° 48′ W	39° 57′ N 70° 48′ W
Depth (Meters)	122	128	140	228	309	359	393	469	680
Sphaeroidina bulloides	13.9	7.9	1.8	1.7	0.1	0.1	0.2		
Globigerina bulloides	19.1	25.5	24.0	30.4	15.8	12.9	10.8	6.2	7.3
Globigerina eggeri	46.6	48.7	54.0	40.0	53.8	66.5	69.6	60.3	80.0
Globigerina inflata	12.7	12.8	17.2	24.2	28.2	17.9	17.6	29.2	11.4
Globigerinoides rubra	2.9	1.2	0.4	0.9	0.3	0.3	0.1		
Globigerinoides sacculifera	1.4	1.8	0.2	0.7	0.2	0.2	0.1		
Globigerinoides conglobata	1.0	0.7	0.5	0.6	0.3	0.8	0.4	1.1	
Orbulina universa	0.2	0.3	0.1	0.2	0.1	0.2	0.1		0.1
Pulleniatina obliquiloculata	0.3	0.7	0.2	0.5	0.2	0.1	0.2		
Globorotalia menardii	1.8	0.4	0.9	0.6	1.0	0.8	0.8	1.8	0.5
Globorotalia hirsuta	0.1		0.1		0.1				
Globorotalia truncatulinoides			0.1	0.1		0.2	0.2	0.6	0.1
Globorotalia tumida			0.5		0.1	0.1	0.1	0.6	0.1
Miscellaneous		0.1							0.3
Estimated number of specimens	35000	188700	38200	282500	82000	18300	13500	6500	83300
Percentage of the planktonic Foraminifera to total fauna	43.1	61.3	74.3	60.8	73.8	76.3	87.1	63.1	71.5

PLATES

PLATE 1

PLATE 1

Species Typical of Zone 2

Fig. 1. *Haplophragmoides major* Cushman. (X36.) Cape Cod Light traverse, 121 m.

Fig. 2. *Eggerella advena* Cushman. (X54.) Cape Cod Light traverse, 103 m.

Figs. 3 a, b. *Quinqueloculina seminulum* (Linnaeus). (X40.) (a, b) opposite sides. Block Id. traverse, 67 m.

Figs. 4 a, b. *Triloculina* sp. (X44.) (a, b) opposite sides. Maryland traverse, 68 m.

Fig. 5. *Quinqueloculina seminulum* (Linnaeus) var. *jugosa* Cushman. (X50.) Maryland traverse, 24.5 m.

Fig. 6. *Ammodiscus* sp. (X40.) Ipswich Bay traverse, 9 m.

Figs. 7 a, b. *Trochammina lobata* Cushman. (X54.) (a) dorsal view; (b) ventral view. New Jersey traverse, 46 m.

Fig. 8. *Globulina inaequalis* Reuss. (X48.) Maryland traverse, 63 m.

Fig. 9. *Pyrgo striatella* (Cushman). (X45.) Maryland traverse, 68 m.

Fig. 10. *Globulina inaequalis* Reuss var. *caribaea* d'Orbigny. (X46.) Maryland traverse, 63 m.

Fig. 11. *Nonion sloanii* (d'Orbigny). (X50.) Maryland traverse, 52 m.

Fig. 12. *Elphidium* sp. (X.46) Maryland traverse, 24.5 m.

Fig. 13. *Bolivina pseudoplicata* Heron-Allen and Earland. (X50.) Maryland traverse, 68 m.

Fig. 14. *Angulogerina* sp. 1. (X54.) New Jersey traverse, 46 m.

Fig. 15. *Discorbis* sp. 2. (X80.) Maryland traverse, 24.5 m.

Figs. 16 a, b. *Cibicides concentrica* (Cushman). (X40.) (a) ventral view; (b) dorsal view. Maryland traverse, 52 m.

Figs. 17 a, b. *Poroeponides lateralis* (Terquem). (X45.) (a) dorsal view; (b) ventral view. Block Id. traverse, 19 m.

1
2
3a
3b
4a
4b
5
6
7a
8
9
10
11
12
13
14
15
16a
16b
17a
17b

PLATE 2

PLATE 2

Species Typical of Zone 3

Fig. 1. *Textularia goessi* Cushman (?). (X44.) Block Id. traverse, 112 m.

Fig. 2. *Textularia pseudotrochus* Cushman. (X30.) Block Id. traverse, 121 m.

Fig. 3. *Gaudryina* (*Pseudogaudryina*) *atlantica* (Bailey). (X24.) Block Id. traverse, 112 m.

Fig. 4. *Trochammina globigeriniformis* (Parker and Jones). (X50.) Maryland traverse, 114 m.

Fig. 5. *Textularia candeiana* d'Orbigny. (X48.) New Jersey traverse, 182 m.

Fig. 6. *Plectina apicularis* (Cushman). (X46.) Block Id. traverse, 97 m.

Fig. 7. *Karreriella affinis* (Fornasini). (X50.) Maryland traverse, 154 m.

Fig. 8. *Massilina* sp. (X50.) Block Id. traverse, 142 m.
120 m.

Fig. 9. *Pyrgo* cf. *denticulata* (H. B. Brady). (X 44.) Block Id. traverse, 120 m.

Fig. 10. *Pyrgo subsphaerica* (d'Orbigny). (X30.) Block Id. traverse, 121 m.

Fig. 11. *Robulus* sp. 3. (X34.) Maryland traverse, 154 m.

Fig. 12. *Robulus* sp. 1. (X44.) Block Id. traverse, 167 m.

Fig. 13. *Robulus* sp. 2. (X45.) Block Id. traverse, 97 m.

Fig. 14. *Pseudoclavulina novangliae* (Cushman). (X40.) Block Id. traverse, 167 m.

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PLATE 3

PLATE 3

Species Typical of Zone 3 (continued)

Fig. 1. *Marginulina bacheii* Bailey. (X40.) Block Id. traverse, 97 m.

Fig. 2. *Pseudopolymorphina atlantica* Cushman and Ozawa. (X54.) Maryland traverse, 114 m.

Fig. 3. *Nonion* cf. *barleeanum* (Williamson). (X50.) Block Id. traverse, 142 m.

Fig. 4. *Nonion grateloupi* (d'Orbigny). (X54.) Block Id. traverse, 142 m.

Figs. 5 a, b. *Discorbis bertheloti* (d'Orbigny). (X46.) (a) dorsal view; (b) ventral view. Block Id. traverse, 142 m.

Figs. 6 a, b. *Nonionella turgida* (Williamson). (X58.) (a, b) opposite sides. Block Id. traverse, 142 m.

Fig. 7. *Robertina* sp. (X48.) Marthas Vineyard traverse, 128 m.

Figs. 8 a, b. *Gyroidina soldanii* d'Orbigny. (X40.) (a) dorsal view; (b) ventral view. Block Id. traverse, 167 m.

Fig. 9. *Epistomina elegans* (d'Orbigny). (X46.) Block Id. traverse, 167 m.

Fig. 10. *Virgulina compressa* (Bailey). (X44.) Marthas Vineyard traverse, 128 m.

Figs. 11 a, b. *Cancris sagra* (d'Orbigny). (X48.) (a) dorsal view; (b) ventral view. Maryland traverse, 99 m.

Fig. 12. *Cassidulinoides bradyi* (Norman). (X42.) Block Id. traverse, 167 m.

Figs. 13 a, b. *Eponides* sp. (X40.) (a) dorsal view; (b) ventral view. Marthas Vineyard traverse, 140 m.

Fig. 14. *Pulvinulinella* cf. *exigua* (H. B. Brady). (X48.) Maryland traverse, 99 m.

Fig. 15. *Chilostomella ovoidea* Reuss. (X50.) Block Id. traverse, 200 m.

Figs. 16 a, b. *Eponides umbonata* (Reuss) var. *ehrenbergi* (Bailey). (X30.) (a) dorsal view; (b) ventral view. Block Id. traverse, 167 m.

Figs. 17 a, b. *Planulina foveolata* (H. B. Brady). (X45.) (a) ventral view; (b) dorsal view. Block Id. traverse, 167 m.

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PLATE 4

PLATE 4

Figures 1–14, Species Typical of Zone 4

Figs. 1, 2. *Valvulina conica* Parker and Jones. (1) (X44.); (2) (X46.). (1) bottom view; (2) apertural view of another specimen. Cape Cod Light traverse, 103 m.

Fig. 3. *Ammosphaeroidina sphaeroidiniformis* (H. B. Brady). (X22.) Marthas Vineyard traverse, 680 m.

Fig. 4. *Listerella nodulosa* (Cushman). (X40.) Marthas Vineyard traverse, 228 m.

Fig. 5. *Karreriella bradyi* (Cushman). (X40.) Marthas Vineyard traverse, 680 m.

Fig. 6. *Pseudoglandulina occidentalis* (Cushman). (X42.) New Jersey traverse, 610 m.

Fig. 7. *Nonion grateloupi* (d'Orbigny) var. (X46.) Marthas Vineyard traverse, 680 m.

Fig. 8. *Bolivina subspinescens* Cushman. (X60.) Marthas Vineyard traverse, 680 m.

Fig. 9. *Bulimina exilis* (H. B. Brady). (X54.) Marthas Vineyard traverse, 680 m.

Fig. 10. *Bulimina marginata* d'Orbigny var. (X40.) Marthas Vineyard traverse, 680 m.

Fig. 11. *Uvigerina peregrina* Cushman. (X34.) Marthas Vineyard traverse, 680 m.

Fig. 12. *Angulogerina angulosa* (Williamson) var. (X52.) Marthas Vineyard traverse, 680 m.

Figs. 13 a, b. *Valvulineria* sp. (X58.) (a) dorsal view; (b) ventral view. Marthas Vineyard traverse, 680 m.

Figs. 14 a, b. *Gyroidina orbicularis* d'Orbigny. (X44.) (a) dorsal view; (b) ventral view. Marthas Vineyard traverse, 680 m.

Fig. 15. *Proteonina difflugiformis* (H. B. Brady). (X46.) Block Id. traverse, 80 m.

Fig. 16. *Haplophragmoides glomeratum* (H. B. Brady). (X48.) Cape Cod Light traverse, 91 m.

Fig. 17. *Haplophragmoides columbiensis* Cushman. (X40.) Cape Cod Light traverse, 103 m.

Fig. 18. *Haplophragmoides subglobosum* (G. O. Sars). (X40.) Ipswich Bay traverse, 71 m.

Fig. 19. *Lagena hexagona* (Williamson). (X48.) Maryland traverse, 154 m.

Fig. 20. *Haplophragmoides* sp. (X40.) Cape Cod Light traverse, 103 m.

Fig. 21. *Spiroplectammina* sp. (X46.) Ipswich Bay traverse, 71 m.

Figs. 22 a, b. *Trochammina globulosa* Cushman. (X46.) (a) dorsal view; (b) ventral view. Cape Cod Light traverse, 103 m.

Fig. 23. *Lagena torquata* H. B. Brady. (X44.) Maryland traverse, 154 m.

Fig. 24. *Lagena laevis* (Montagu) var. nebulosa Cushman. (X48.) Maryland traverse, 154 m.

Fig. 25. *Lenticulina peregrina* (Schwager). (X54.) Marthas Vineyard traverse, 228 m.

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PLATE 5

PLATE 5

Species Not Confined to One Zone

Fig. 1. *Dentalina mucronata* (Neugeboren). (X42.) Block Id. traverse, 167 m.

Fig. 2. *Nodosaria pyrula* d'Orbigny. (X50.) Block Id. traverse, 167 m.

Fig. 3. *Guttulina lactea* (Walker and Jacob). (X30.) Maryland traverse, 63 m.

Fig. 4. *Elphidium subarcticum* Cushman. (X42.) Maryland traverse, 49 m.

Fig. 5. *Nonion labradoricum* (Dawson). (X52.) Block Id. traverse, 142 m.

Fig. 6. *Astrononion stellatum* Cushman and Edwards. (X44.) Cape Cod Light traverse, 144 m.

Fig. 7. *Elphidium incertum* (Williamson). (X40.) Maryland traverse, 49 m.

Fig. 8. *Robertina arctica* d'Orbigny. (X42.) Cape Cod Light traverse, 121 m.

Fig. 9. *Bulimina* (*Desinobulimina*) *auriculata* Bailey. (X38.) Cape Cod Light traverse, 203 m.

Fig. 10. *Bulimina* (*Desinobulimina*) *turgida* Bailey. (X30.) Marthas Vineyard traverse, 680 m.

Fig. 11. *Bulimina marginata* d'Orbigny. (X42.) Block Id. traverse, 142 m.

Fig. 12. *Bulimina aculeata* d'Orbigny. (X45.) Marthas Vineyard traverse, 680 m.

Fig. 13. *Bulimina* sp. (X50.) Maryland traverse, 99 m.

Fig. 14. *Virgulina* sp. (X50.) Marthas Vineyard traverse, 359 m.

Fig. 15. *Virgulina fusiformis* Williamson. (X48.) Marthas Vineyard traverse, 228 m.

Fig. 16. *Bolivina* sp. 1. (X50.) Marthas Vineyard traverse, 128 m.

Fig. 17. *Bolivina subaenariensis* Cushman. (X50.) Maryland traverse, 154 m.

Fig. 18. *Bolivina* sp. 2. (X48.) Maryland traverse, 154 m.

Fig. 19. *Uvigerina* sp. (X50.) Block Id. traverse, 112 m.

Fig. 20. *Uvigerina peregrina* Cushman var. *bradyana* Cushman. (X54.) Block Id. traverse, 112 m.

Fig. 21. *Angulogerina angulosa* (Williamson). (X50.) Block Id. traverse, 112 m.

Fig. 22. *Angulogerina* sp. 2. (X50.) Cape Cod Light traverse, 203 m.

Figs. 23 a, b. *Discorbis floridana* Cushman. (X54.) (a) dorsal view; (b) ventral view. Maryland traverse, 99 m.

Figs. 24 a, b. *Discorbis obtusa* d'Orbigny. (X44.) (a) dorsal view; (b) ventral view. Maryland traverse, 99 m.

Figs. 25 a, b. *Eponides frigida* (Cushman) var. *calida* Cushman and Cole. (X46.) (a) dorsal view; (b) ventral view. Block Id. traverse, 97 m.

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PLATE 6

PLATE 6

Species Not Confined to One Zone

Figs. 1 a, b. *Eponides umbonata* (Reuss). (X52.) (a) dorsal view; (b) ventral view. Block Id. traverse, 167 m.

Figs. 2 a, b. *Cassidulina norcrossi* Cushman. (X46.) (a, b) opposite sides. Maryland traverse, 154 m.

Figs. 3 a, b. *Cassidulina subglobosa* H. B. Brady. (X46.) (a, b) opposite sides. Maryland traverse, 154 m.

Fig. 4. *Cassidulina laevigata* d'Orbigny. (X50.) Maryland traverse, 154 m.

Figs. 5 a, b. *Cassidulina crassa* d'Orbigny. (X50.) (a, b) opposite sides. Maryland traverse, 154 m.

Figs. 6 a, b. *Cassidulina* sp. (X42.) (a, b) opposite sides. Maryland traverse, 99 m.

Figs. 7 a, b. *Cibicides pseudoungeriana* (Cushman). (X46.) (a) dorsal view; (b) ventral view. Block Id. traverse, 167 m.

Fig. 8. *Pullenia quinqueloba* (Reuss). (X48.) Maryland traverse, 154 m.

Figs. 9 a, b. *Planulina mera* Cushman. (X40.) (a) ventral view; (b) dorsal view. Maryland traverse, 52 m.

Figs. 10 a, b. *Cibicides refulgens* (Montfort). (X42.) (a) ventral view; (b) dorsal view. Maryland traverse, 52 m.

Fig. 11.[1] *Orbulina universa* d'Orbigny. (X46.) Marthas Vineyard traverse, 309 m.

Figs. 12, 13. *Globigerina inflata* d'Orbigny. (X46.) (12) dorsal view; (13) ventral view of another specimen. Marthas Vineyard traverse, 309 m.

[1] Figures 11–13 are planktonic forms.

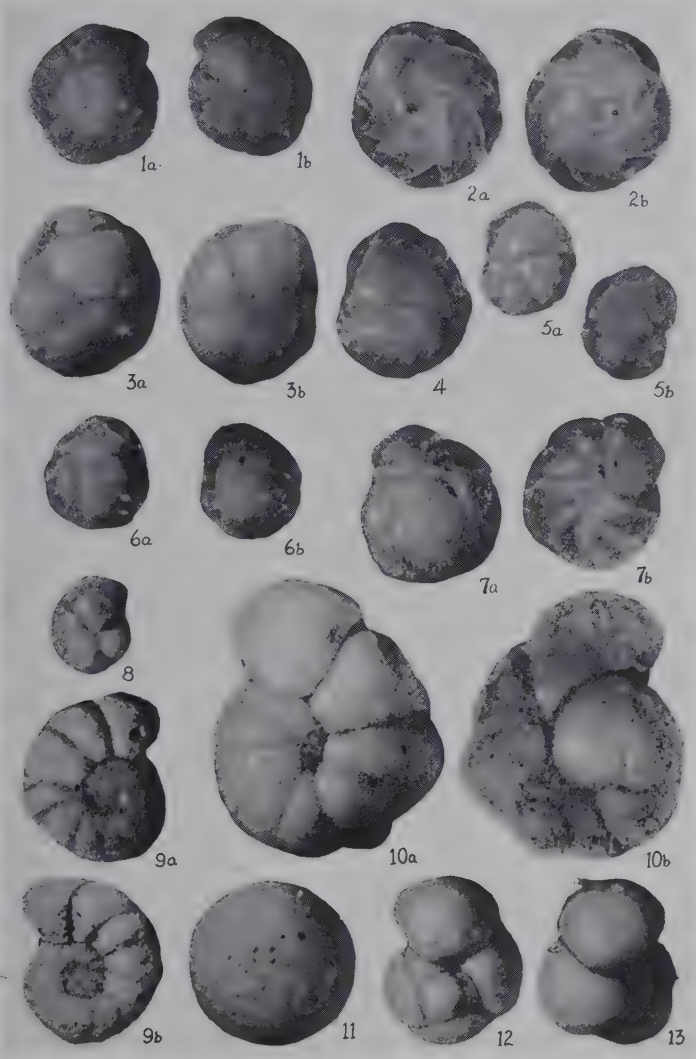
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PLATE 7

PLATE 7

Planktonic Species

Figs. 1, 2. *Globigerina bulloides* d'Orbigny. (X48.) (1) dorsal view; (2) ventral view of another specimen. Marthas Vineyard traverse, 309 m.

Fig. 3. *Sphaeroidina bulloides* d'Orbigny. (X48.) Block Id. traverse, 200 m.

Fig. 4. *Globigerinoides rubra* (d'Orbigny). (X48.) Marthas Vineyard traverse, 309 m.

Figs. 5, 6. *Globigerina eggeri* Rhumbler. (X44.) (5) dorsal view; (6) ventral view of another specimen. Marthas Vineyard traverse, 309 m.

Fig. 7. *Globigerinoides sacculifera* (H. B. Brady). (X50.) Marthas Vineyard traverse, 309 m.

Figs. 8, 9. *Globigerinoides conglobata* (H. B. Brady). (X44.) (8) dorsal view; (9) ventral view of another specimen. Marthas Vineyard traverse, 309 m.

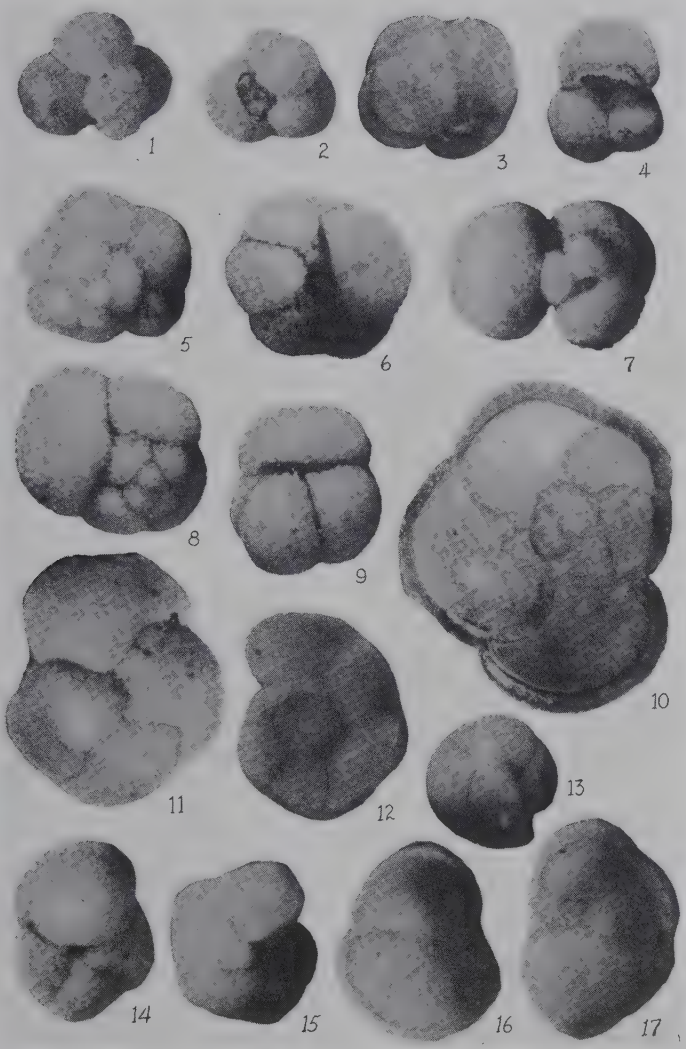
Fig. 10. *Globorotalia menardii* (d'Orbigny). (X44.) Marthas Vineyard traverse, 309 m.

Figs. 11, 14. *Globorotalia hirsuta* (d'Orbigny). (11) (X50.); (14) (X52.). (11) dorsal view; (14) ventral view of another specimen. Block Id. traverse, 200 m.

Figs. 12, 15. *Globorotalia truncatulinoides* (d'Orbigny). (X50.) (12) dorsal view; (15) ventral view of another specimen. Marthas Vineyard traverse, 309 m.

Fig. 13. *Pulleniatina obliquiloculata* (Parker and Jones). (X48.) Marthas Vineyard traverse, 309 m.

Figs. 16, 17. *Globorotalia tumida* (H. B. Brady). (X46.) (16) ventral view; (17) dorsal view of another specimen. Marthas Vineyard traverse, 309 m.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Contribution No. 380

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INDUSTRIAL AND ENGINEERING CHEMISTRY,
Vol. 40, Page 450, March, 1948
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Chlorine and Sodium Pentachlorophenate as Fouling Preventives in Sea Water Conduits

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Continuous chlorination with residual concentrations as low as 0.25 part per million prevents the attachment and growth of slime bacteria and macroorganisms in sea water circulating systems. Some adult mussels and anemones may survive 10 days of intermittent chlorination with residual concentrations as high as 10.0 parts per million even when the periods of treatment are as long as 8 hours per day. Sodium pentachlorophenate prevents the attachment and growth of macroorganisms but is ineffective in eliminating slime when concentrations as low as 1.0 part per million are maintained continuously. The relative merits of chlorine and sodium pentachlorophenate are discussed.

PIPES and conduits used to transport sea water in ships and industrial power plants are frequently subject to marine fouling. Such growths reduce the efficiency of cooling systems, and when they occur in fire mains, they create serious hazards. The design of the system must provide for periodic cleaning, and clean-

ing operations with their attendant shutdowns are themselves expensive. Dobson (*1*) recently reviewed the various methods which have been tried or suggested for the control of such fouling. He concluded that the most promising treatment is the injection of chlorine into the sea water. Such treatment appears to be quite effective against slime-forming organisms which directly interfere with heat transfer in condensers. In some cases it has given promise of controlling the growth of macro-organisms in pipe systems.

Although a number of installations have been made for the control of fouling by means of chlorine, there appears to be no published record of studies designed to determine experimentally the concentrations and periods of treatment which are required to prevent fouling efficiently. Such experiments have been conducted recently by the Woods Hole Oceanographic Institution. The results of these experiments are reported here. They give some indication of what may be expected from various methods of treatment and also suggest an explanation of failures which sometimes occur in industrial practice.

The antifouling properties of an organic toxic, sodium pentachlorophenate, were also investigated to determine if this material could be used where chlorine might be unsuitable.

EXPERIMENTS WITH CHLORINE

Intermittent Treatment. The first experiment, performed at Woods Hole, Mass., determined the killing power of various concentrations of chlorine when applied both intermittently and continuously to adult organisms (*4*). Battery jars containing organisms of representative species were subjected to the following treatment: One jar, serving as a control, was circulated continuously with fresh sea water. Four jars were irrigated periodically with sea water containing chlorine in a residual concentration of 10 parts per million on a schedule of 1, 2, 4, and 8 hours each day. The rest of the time the jars were circulated with untreated sea water. The sixth jar was flushed continuously with the chlorinated water. (Chlorine was applied as a solution of calcium hypochlorite, introduced into the sea water main by means of a proportionating pump.) After 10 days of this treatment, the organisms in all six jars were flushed continuously for 10 more days with unchlorinated sea water to allow for delayed effects to develop.

The results of this experiment are given in Table I. Intermittent exposures for periods as long as 8 hours per day with 10 p.p.m. chlorine were ineffective against mussels and anemones, and the 4-hour periods did not completely eliminate all the barnacles. The tunicates and bryozoa were all killed by exposure for 1 hour per day. This short treatment was sufficient to prevent the formation of slime on the sides of the jars.

Continuous Treatment. Since intermittent treatment with daily exposures as long as 8 hours per day was ineffective against some forms, an experiment was performed to determine the killing times of different chlorine concentrations when applied continuously. Three series of jars containing fouling organisms

TABLE I. PERCENTAGE OF SURVIVAL OF FOULING ORGANISMS DURING AND AFTER PERIODIC TREATMENT WITH CHLORINATED SEA WATER CONTAINING 10 P.P.M. RESIDUAL CHLORINE

Hr. Treatment/ Day	Animals	% Survival after Treatment of 1 day	2 days	3 days	4 days	5 days	6 days	7 days	8 days	9 days	10 days	20 days
0	Anemones	100	100	100	100	..	100	100	100	100	100	100
	Mussels	100	100	100	..	..	100	100	100	100	100	100
	Barnacles	100	100	..	85	..	85	..	..	..	85	85
	Molgula	100	..	100	..	..	..	100	..	..	100	90
	Botryllus	100	..	75	..	..	..	75	..	..	75	0
	Bugula	100	..	100	..	..	100	..	..	..	50	50
1	Anemones	100	100	100	100	100	100	100	100	100	100	100
	Mussels	100	100	100	100	95	95	95	95	95	95	95
	Barnacles	100	25	25	10	10	10	10	10	10	10	0
	Molgula	75	50	50	5	5	5	5	5	5	0	0
	Botryllus	20	20	..	..	10	10	10	0	0	0	0
	Bugula	50	..	..	..	0	0	0	0	0	0	0
2	Anemones	100	100	100	100	100	100	100	100	100	100	100
	Mussels	100	100	100	100	100	100	100	100	100	100	100
	Barnacles	100	65	10	10	10	10	10	10	10	10	5
	Molgula	75	20	10	10	0	0	0	0	0	0	0
	Botryllus	20	10	..	..	0	0	0	0	0	0	0
	Bugula	50	..	..	..	0	0	0	0	0	0	0
4	Anemones	100	100	100	100	100	100	100	100	100	100	100
	Mussels	100	100	100	100	100	100	100	100	100	100	100
	Barnacles	100	75	50	10	10	10	7	7	7	5	5
	Molgula	75	20	10	10	0	0	0	0	0	0	0
	Botryllus	20	0	0	0	0	0	0	0	0	0	0
	Bugula	10	..	..	..	0	0	0	0	0	0	0
8	Anemones	100	100	100	100	100	100	100	100	100	100	100
	Mussels	100	100	100	100	100	100	100	100	100	100	100
	Barnacles	65	65	50	10	0	0	0	0	0	0	0
	Molgula	75	10	10	10	0	0	0	0	0	0	0
	Botryllus	20	..	0	0	0	0	0	0	0	0	0
	Bugula	10	..	..	..	0	0	0	0	0	0	0
24[a]	Anemones	100	..	..	..	0	100[a]	100	100	50	0	..
	Mussels	50	..	..	..	0	100[a]	90	50	10	2	0
	Barnacles	25	..	..	..	0	50[a]	10	0	0	0	..
	Molgula	10	..	..	..	0	25[a]	25	0	0	0	..
	Botryllus	0	..	..	..	0	10[a]	10	0	0	0	..
	Bugula	10	..	..	..	0	10[a]	..	0	0	0	..

[a] The population of this jar was renewed on the sixth day after all the dead organisms had been removed and the jar cleaned.

TABLE II. PERCENTAGE SURVIVAL OF ORGANISMS AFTER CONTINUOUS TREATMENT WITH CHLORINATED SEA WATER OF VARIOUS STRENGTHS AND FOR VARIOUS TIMES

Chlorine Concn., P.P.M.	Animal	% Survival after Treatment of 0 day	1 day	2 days	3 days	4 days	5 days	6 days	7 days	8 days	9 days	12 days	15 days
10	Anemones	100	100	100	50	0	0	..	..	..	..	..	..
	Mussels	100	95	65	35	10	0	..	..	..	..	..	..
	Barnacles	90	20	20	0	2	0	..	..	..	..	..	..
	Molgula	100	0	0	0	0	0	..	..	..	..	..	..
	Bugula	100	0	0	0	0	0	..	..	..	..	..	..
2.5	Anemones	100	100	100	100	75	60	50	..	0	..	..	..
	Mussels	95	95	85	35	20	0	0	..	0	..	..	..
	Barnacles	100	50	25	5	0	0	2	..	0	..	..	..
	Molgula	100	0	0	0	0	0	0	..	0	..	..	..
	Bugula	100	..	0	0	0	0	0	..	0	..	..	..
1	Anemones	100	100	100	100	..	100	..	100	..	100	100	100
	Mussels	100	100	75	65	..	45	..	35	..	50	15	0
	Barnacles	100	90	90	50	..	25	..	0	..	50	2	20
	Molgula	100	100	100	0	..	0	..	0	..	0	0	0

were circulated with sea water containing residual chlorine concentrations of 1.0, 2.5, and 10.0 p.p.m., respectively. One jar from each series was removed each day and supplied with fresh running sea water. The survival times of the different species are given in Table II. The two higher chlorine concentrations were lethal to all organisms in 5 to 8 days. Anemones, mussels, and barnacles survived longest. A few mussels survived 12 days of treatment with 1.0 p.p.m., and a few barnacles and all the anemones were alive after 15 days.

Prevention of Attachment. Since the larvae are generally considered to be more delicate than adults, it was believed that somewhat lower chlorine concentrations might be effective in preventing their attachment. To test the effect of continuous dosage on attachment and subsequent growth under conditions comparable with industrial practice, experimental pipe systems were set up in Miami, Fla. (*5*). These units consisted of a 6-foot length of 3-inch galvanized iron pipe. A rubber hose dipping below the surface of Biscayne Bay served as an intake. Sea water was sucked through the units by means of gear pumps mounted in the outflow. Glass plates were inserted into the pipe to serve as collectors of fouling. Calcium hypochlorite solution was injected near the intake by means of a proportionating pump, and the residual concentration was checked at the outflow. The rate of flow was maintained at 2 gallons per minute with a chlorine residual of 1.0 p.p.m. One untreated unit served as a control. During 2 months' operation the glass test plates inserted into the control system fouled heavily, while those in the treated system remained entirely free of organisms.

Another experiment designed to determine the minimum concentration which would be effective was conducted at Kure Beach, N. C. (*6*). Six similar units of steel pipe were flushed continuously from a common source of sea water. Each emptied into a weir box used to control the rate of circulation. Chlorine gas was injected into the sea water so that chlorine residuals of 1.5, 1.0, 0.75, 0.5, and 0.25 p.p.m. were maintained in respective units of the apparatus. One unit was untreated as a control. The velocity of flow varied in different parts of each unit from 8.6 to 1.3 feet per second and was lower in the weir box. During 3 months' operation abundant fouling occurred on test panels in the weir box of the control unit and in all parts of the system where the velocity of flow was 1.72 feet per second or less. No fouling occurred in any of the chlorinated units. This indicated that 0.25 p.p.m. was above the effective minimum, and also showed that attachment and growth of fouling can be prevented by continuous application of concentrations of chlorine much lower than those which permit adults to survive even after a considerable period of exposure. It also lends support to the belief that such fouling organisms as mussels are less resistant in the larval stages.

EXPERIMENTS WITH SODIUM PENTACHLOROPHENATE

In a preliminary experiment to determine the general order of toxicity of sodium pentachlorophenate a 5% stock solution of

TABLE III. CONDITION OF ORGANISMS AFTER VARIOUS TIMES OF EXPOSURE TO DILUTIONS OF SODIUM PENTACHLOROPHENATE IN SEA WATER

Concn., P.P.M.	Animal	Condition[a] after Exposure of 0 hr.	1 hr.	7 hr.	18 hr.	22 hr.	27 hr.	43 hr.	53 hr.	65 hr.	91 hr.	115 hr.
0	Mussels	x	x	xx	xx	xx	xx	xx	xx	xx	xx	xx
	Anemones	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
	Barnacles	xx	xx	x	xx	x	xx	xx	xx	xx	xx	xx
0.1	Mussels	xx	x	xx	xx	xx	xx	x	x	x	xx	xx
	Anemones	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
	Barnacles	x	xx	xx	xx	xx	xx	x	x	xx	x	x
1.0	Mussels	x	x	xx	xx	x	x	x	x	x	—	—
	Anemones	xx	xx	xx	xx	xx	x	x	x	—	—	—
	Barnacles	xx	xx	x	x	x	x	x	x	—	—	—
10	Mussels	x	x	x	x	x	x	—	—	—	—	—
	Anemones	x	x	x	x	x	—	—	—	—	—	—
	Barnacles	xx	x	—	—	—	—	—	—	—	—	—
100	Mussels	x	x	x	x	x	x	x	—	—	—	—
	Anemones	x	x	—	—	—	—	—	—	—	—	—
	Barnacles	x	x	—	—	—	—	—	—	—	—	—
1000	Mussels	x	x	—	—	—	—	—	—	—	—	—
	Anemones	x	—	—	—	—	—	—	—	—	—	—
	Barnacles	—	—	—	—	—	—	—	—	—	—	—

[a] xx = quite active—barnacles filter, anemones wide open, mussels siphon; x = inactive but alive—barnacles just "breathe," mussels and anemones shut; — = dead—barnacles rigidly open or shut, mussels wide open, anemones usually decomposing.

sodium pentachlorophenate (Santobrite) in distilled water was added to sea water in quantities sufficient to give solutions ranging from 0.1 to 1000 p.p.m. The solutions containing 100 and 1000 p.p.m. formed precipitates and consequently did not retain the original concentration. Mussels, barnacles, and anemones were placed in each solution, and the solutions were changed twice daily to remove waste materials and maintain the oxygen supply. The condition of the animals at subsequent times is given in Table III.

The experiment showed that dilutions of 0.1 p.p.m. were ineffective but those of 1.0 p.p.m. killed all the organisms in less than 3 days. Stronger solutions killed in shorter times.

To secure a more exact comparison of the toxicity of sodium pentachlorophenate and chlorine, a solution of the former (*4*) was injected into running sea water at rates which yielded concentrations of 10 and 1.0 p.p.m. Animals were then exposed to these concentrations continuously in a manner similar to tha employed in the experiment made at Woods Hole with various concentrations of chlorine. The percentage of organisms surviving after various intervals is given in Table IV.

This experiment demonstrated that the toxicity of sodium pentachlorophenate is of the same general order as is that of chlorine, and that it is somewhat more effective against the hardier forms in the concentration of 1 p.p.m.

When the experimental pipe system was set up for the experiments with chlorine at Miami, Fla., the effects of continuous application of sodium pentachlorophenate on the attachment and growth of organisms were tested at the same time. A solution of sodium pentachlorophenate was injected by one of the pumps

TABLE IV. PERCENTAGE SURVIVAL OF ORGANISMS AFTER CONTINUOUS TREATMENT WITH SEA WATER CONTAINING SODIUM PENTACHLOROPHENATE

Concn. Pentachlorophenate, P.P.M.	Animal	% Survival after Treatment of							
		0 day	1 day	2 days	3 days	4 days	5 days	6 days	7 days
10	Anemone	100	0	0	0	0	0	0	0
	Mussel	100	95	50	10	4	0	0	0
	Barnacle	75	25	5	0	0	0	0	0
	Molgula	100	0	0	0	0	0	0	0
	Bugula	100	0	0	0	0	0	0	0
1.0	Anemone	100	100	100	20	0	0	0	0
	Mussel	100	100	15	0	0	0	0	0
	Barnacle	80	35	10	10	0	0	0	0
	Molgula	100	0	0	0	0	0	0	0
	Bugula	100	0	0	0	0	0	0	0

of the proportionator into a unit identical to the control and chlorinated units in an amount calculated to maintain the concentration in the pipes at 1.0 p.p.m. When the experiment was terminated after 2 months' operation, no macroscopic fouling had appeared but there was a deposit of slime in the pipes. The experiment indicated that sodium pentachlorophenate is comparable to chlorine in preventing attachment and growth of macro-organisms but is ineffective against slime-forming organisms.

The effective dosage of sodium pentachlorophenate was tested further at Kure Beach simultaneously with the chlorination experiment. By means of Wallace and Tiernan hypochlorinators, two units identical with those used in the chlorination experiment were fed continuously sufficient stock solution of sodium pentachlorophenate (Dowicide G) to result in concentrations of 0.5 and 1.0 p.p.m. The higher concentration satisfactorily inhibited macroscopic fouling, while the lower one permitted a moderate growth. This demonstrated that the minimum lethal dosage lies between those concentrations. In both units there was a considerable accumulation of slime in the pipes and weir boxes and on test plates.

CONCLUSIONS

The experiments indicate that continuous chlorination with residuals as low as 0.25 p.p.m. should give complete control of fouling in sea water circulating systems. Harbor water commonly contains enough organic matter to produce chlorine demands of 2 or 3 p.p.m., and where pollution is heavy the demand is considerably greater. Consequently it appears that the chlorine requirement is set essentially by the chlorine demand of the water and that a chlorine dosage slightly in excess of this demand may be expected to control fouling.

The minimum dosage of sodium pentachlorophenate which will prevent attachment and growth of marine animals when applied continuously is 1 p.p.m. This is a net figure which presumably does not need to be supplemented by an allowance for organic matter present in the sea water. Pentachlorophenate

may consequently be an acceptable substitute for chlorine in preventing the development of clogging growths, especially when the chlorine demand of the water is great. On the other hand, it is inferior to chlorine in controlling the development of slime in condenser tubes. Otherwise the relative merits of chlorine and pentachlorophenate will depend on a variety of factors, including cost, the question of corrosion, and the convenience and hazards involved in handling the materials, which depend on the size and nature of the installation in question.

Where large volumes of sea water are used, the cost of continuous treatment with chlorine has proved to be greater than the expense of periodic cleaning of the conduits. Attempts to control fouling more economically by intermittent treatment have succeeded in preventing the formation of bacterial slimes in condenser tubes and appear to be profitable because of the improved efficiency of heat transfer which results (*1*). Such treatment has sometimes failed to control the growth of marine animals.

Along the Atlantic coast north of Cape Hatteras the most serious fouling in sea water conduits is due to the mussel, *Mytilus edulis*. The experiment with intermittent treatment described here shows that adult mussels are able to resist relatively heavy daily dosages of chlorine if applied intermittently with a considerable interval without treatment intervening. It is apparent that if adult mussels are once permitted to become established, intermittent treatments may be ineffective in dislodging them or preventing their continued growths.

Nothing appears to be known of the susceptibility of mussel larvae to intermittent treatments with chlorine. According to Matthews (*3*) and Field (*2*), mussels first attach during a stage when the larvae are still equipped with swimming organs but are already enclosed by shells. It is possible that, by closing the shell, these larvae may protect themselves during intermittent periods of chlorination as the adults are observed to do. Any attempt to reduce effectively the expense of chlorination by intermittent treatment should be based on the determination of the susceptibility of the mussel during the early stages of attachment to chlorine which is applied in intermittent dosages of various durations and strength.

ACKNOWLEDGMENT

The proportionating pump used in the chlorine experiments at Woods Hole was loaned by % Proportioneers, Inc. %, Providence, R. I., through the kindness of Jeff Corydon. The equipment used at Kure Beach was supplied by Wallace and Tiernan, Inc., through the kindness of R. B. Martin, and consisted of their type MSP chlorinators. The location and facilities were supplied by the Ethyl Dow Corporation and were arranged for by F. L. LaQue of the International Nickel Company. The sea water was drawn from the intake canal of the Ethyl Dow plant. The Dowicide G was supplied by John V. Grebe of the Dow Chemical Company.

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RECEIVED April 9, 1947. Contribution No. 380 of the Woods Hole Oceanographic Institution. This work was done under a contract between the Institution and the Bureau of Ships, Navy Department. The interest of H. A. Ingram, U.S.N., in initiating the study is gratefully acknowledged. The opinions presented here are those of the authors and do not necessarily reflect the official opinion of the Navy Department or the naval service at large.

PRINTED IN U. S. A.

Contribution No. 389

NOTE CONCERNING HUMAN RESPIRATORY IRRITATION ASSOCIATED WITH HIGH CONCENTRATIONS OF PLANKTON AND MASS MORTALITY OF MARINE ORGANISMS[1]

By

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There is increasing evidence that high concentrations of plankton are sometimes associated with mass mortality among marine animals (Taylor, 1917, see ref's pp. 14–16; Marchand, 1928; Brongersma-Sanders, 1947; Gunter, et al., 1947).

Human respiratory irritations, also concurrent with mass mortality of fish, have been recorded by Taylor (1917), Lund (1934–35), and Gunter, et al. (1947). The respiratory irritant, commonly termed a gas, is said to produce hard coughing and a burning sensation in the nose, throat and lungs. This irritation is reported to occur in persons near the shore during onshore winds, as well as on the open sea.

This paper gives support to the work of Somner, et al. (1937), which indicates that certain dinoflagellates produce irritating or poisonous effects when present in high concentrations. It is the purpose of this paper to list qualitative subjective tests which show that the above-mentioned respiratory irritation is associated with the presence in the inhaled air of minute drops originating in sea water discolored by high concentrations of dinoflagellates.

The presence of sea water nuclei in oceanic air under ordinary conditions is well known (Owens, 1926; Jacobs, 1937, 1939; Cunningham, 1942; and Dessens, 1947). These nuclei are sometimes crystalline, sometimes liquid, depending upon the relative humidity of the ambient air. This phase change usually occurs somewhere between 60 and 75% relative humidity (Owens, 1926; Wright, 1939; and Dessens, 1947). The nuclei vary in radius from about 0.3 to 30μ. These aerosols from the sea are probably formed by bursting bubbles from breaking waves in a manner similar to that shown to occur in effervescing H_2O (Stuhlman, 1932). Zobell (1940) has found that marine bacteria exist in oceanic air and he suggests that they are carried into the air by sea water nuclei produced by spray. Therefore it is reasonable to suppose

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that other organisms or products of the sea are also carried up from the sea surface film by these spray drops.

At the request of the United States Fish and Wildlife Service, the author visited Venice, Florida in July 1947 when great numbers of fish were dying along the local shores of the Gulf of Mexico. Light offshore winds prevailed at this time and reports of human respiratory irritations[2] had recently ceased. Since the presence of this irritation was reported as associated with "red water," dying fish and onshore winds, it was reasonable to test some of the discolored water. During July and August 1947 the following simple tests and experiences were recorded.

Samples of sea water of a deep reddish shade were taken on July 24, 1947, about 5 miles offshore[3] at Lat. 27° 14′ 15″ N., Long. 82° 39′ 10″ W. These samples were unconcentrated sea water collected by dip-bucket. They were found to contain from 15 to 56 million dinoflagellates per liter. (The greatest number, *i. e.* 56 x 10^6 dinoflagellates per liter, is about four times the maximum reported by Allen [1941] in a twenty years' statistical study of marine dinoflagellates of southern California). These dinoflagellates were about 25 microns in diameter and were identified as *Gymnodinium* sp. by F. G. Walton Smith and Paul S. Galtsoff (personal communications). When sea water containing 56 x 10^6 dinoflagellates per liter was sprayed into the nose and throat with a hand atomizer, coughing and a burning sensation in the nose and throat resulted. This effect is apparently similar to that experienced along local beaches during onshore winds. This test was repeated many times with the same results. Relatively clear sea water from another local area produced no similar irritation.

During July 24 and 25, 1947, the author and two companions spent about five hours at sea, near and immediately over large patches of "red water." For long periods of time we worked over tubs of this water, over nets slimy with concentrated plankton and decks awash with spilled "red water." Winds during this time did not exceed 3 m/sec and there were no white caps on the sea surface. We noted no respiratory trouble of any kind throughout this period. However, on the afternoon of the 24th a thunder squall with heavy rain and a force 5 wind (from the east) passed over. During this squall, of about 30 minutes duration, the sea surface became streaked with foam, which was presumably caused by breaking waves and the impact of heavy rain on the surface water. During the latter part of the passage of

[2] Detailed information concerning the objective symptoms of this respiratory irritation may be secured from Dr. T. S. Thompson, M.D., Box 224, Venice, Florida.

[3] "Red water" from this area was found to contain unusually high concentrations of phosphorus (see Ketchum and Keen, 1948).

this squall we experienced coughing and a burning sensation in the nose and throat. After the wind subsided and the white caps and foam streaks disappeared, the respiratory irritation also disappeared. Thus the presence of an irritant in the free air over the "red water" seemed to be correlated with increased wind and with the presence of breaking waves and foam. Sampling of aerosols at this time was prevented by the rain.

About 20 cm.^{3} of the sea water containing 56 x 10^6 dinoflagellates per liter was passed through a Jena fritted glass bacteria filter which had 1 to 1.5 micron openings. This filtrate produced the same irritation as did the unfiltered water when it was sprayed into the nose and throat with an atomizer. No particulate matter was seen in this filtrate under the microscope, using a magnification of 500×.

Samples of the "red water" were placed in shallow aluminum pans and heated. At temperatures varying from 80° to 90° C, clouds of fine bubbles formed in this water. These bubbles rose to the surface and burst, causing the hissing sound of effervescence. Coincident with the formation of these clouds of small bursting bubbles, the vapor rising from the surface produced involuntary coughing and a burning sensation in the nose and throat. When the heat source was removed, the bubbling quickly ceased and the irritating effects of the vapor also ceased. Upon reapplication of the heat and the reformation of the clouds of fine bubbles, the irritating effect of the vapor was again present. When the relatively clear sea water was heated in this manner, no irritating effects could be detected upon inhaling the vapors.

Small (1 x 10 mm.) glass slides, covered with a hydrophobic film, were exposed for 10 seconds at a height of 2 cm. above various vessels, some containing clear sea water and others containing "red water," under different conditions of temperature and effervescence. Table I

TABLE I.

	"Red Water"				*Relatively Clear Sea Water*			
	Bubbling		*No Bubbles*		*Bubbling*		*No Bubbles*	
T°C	*26°*	*85°–95°*	*26°*	*85°–95°*	*25°*	*85°–95°*	*25°*	*85°–95°*
Drop diameters (microns)	15–80 (estimate)	15–80 (estimate)	no drops	no drops	15–80	15–80	no drops	no drops
Respitory Irritation	Yes	Yes	No	No	No	No	No	No

shows the conditions under which drops were or were not deposited on these glass slides, the size range of these drops,[4] and the occurrence of

[4] The isopiestic technique used to cause these small drops to assume their original concentration and size under the microscope will be described in a later publication.

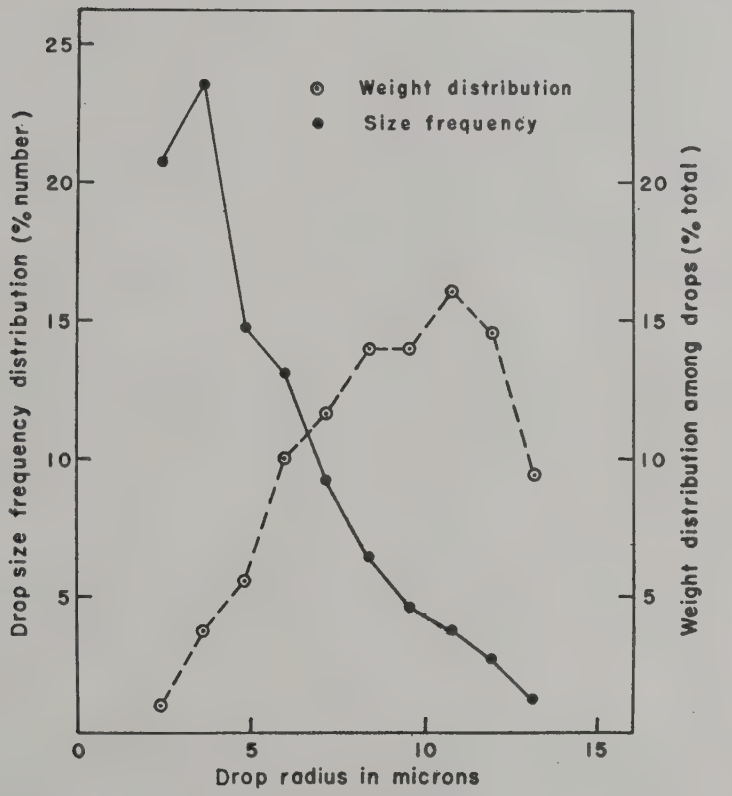

Figure 4. Approximate distribution of size and weight of sea water aerosols over Venice Beach, Fla., July 28, 1947. Sampling height 2 m, 50 m back from the edge of the sea. Wind velocity 4.2 m/sec south. Surf light.

respiratory irritation resulting from inhaling air from immediately over the various water samples.

In order to produce effervescence at room temperatures, a Pasteur-Chamberlain unglazed porcelain filter was placed in "red water," and air was forced through it under a pressure of 1.6 kg/cm^2. Clouds of fine bubbles were produced which, upon rising to the surface and bursting, formed a haze of drops in the air. Breathing this haze produced irritation of the nose and throat, though this effect was not as intense as that resulting from breathing vapor over effervescing heated "red

water." Similar tests with relatively clear sea water produced no irritation. The volume of sea water and "red water" used in these tests was about 2 liters and the water surface area exposed was about 200 cm^2.

When a pad of absorbent cotton 2 cm. thick was held over the mouth and nose, air inhaled from over effervescent "red water," heated or unheated, produced no irritation. This indicates that the irritant, as it exists in the air-borne form, can be reduced by filtration to a concentration which is not detectable when inhaled.

On the afternoon of July 28, 1947, the wind over Venice Beach shifted to the south (an onshore wind) and a slight throat irritation was noticed by the author and others. Glass slides (1 x 10 mm.) were exposed, normal to a measured flow of wind. Corrected counts (under a microscope) of the drops impinged upon these slides revealed a concentration of 112 drops per liter of air.[5] Fig. 4 shows the approximate size and weight distribution of the drops collected on a slide at this time. The weight of salt and water present was about 1.4×10^{-7} grams per liter of air. The method used in deriving these values is based in part upon the work of Houghton and Radford (1938), Langmuir (1944) and Langmuir and Blodgett (1945). An account of this method will be given in a later publication.

Unconcentrated "red water" containing 56×10^6 dinoflagellates per liter was stored for several weeks in well filled 19 liter bottles without preservatives. This water was found to retain its irritating qualities apparently unimpaired.

SUMMARY

1. Nose and throat irritations, similar to those naturally occurring in the Venice Beach region of the Gulf coast of Florida during July 1947, can be produced by breathing air artificially laden with small drops of the Gulf of Mexico water which contains (or contained) 56×10^6 dinoflagellates per liter.
2. The presence of naturally produced drops of sea water in the air along Venice Beach, Florida, during a time when respiratory irritation occurred, is indicated. Approximate drop size range and concentration is given.
3. Simple experiments show that respiratory irritation is always associated with the presence of small drops of "red water" in the air.
4. "Red water" stored without preservative for several weeks retained its irritating qualities apparently undiminished. The persistence of the irritant through weeks of storage without preservative and

[5] During heavy surf conditions, with onshore wind, concentrations as high as 3,000 drops per liter of air have been measured by the author.

through large temperature changes indicates a rather stable substance.

5. Drops from effervescing heated "red water" were more irritating than drops from effervescing water at room temperature, and these later drops seemed more irritating than spray drops produced by the hand atomizer.
6. The irritant passed through a fine bacteria filter (1 to 1.5 micron openings).
7. When air-borne, the irritant can be so reduced in concentration, by inhaling through absorbent cotton, that it ceases to affect the respiratory system.

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Contribution No. 390

Reprinted from Ecology, Vol. 29, No. 1, January, 1948
Printed in U. S. A.

AN OBSERVATION ON THE INHIBITION OF MARINE WOOD DESTROYERS BY HEAVY FOULING ACCUMULATION[1]

In the exposure of wood frames and wood test samples in the waters of southern Florida, considerable variation in the attack of the wood by wood-destroying marine organisms was noted. Greatest destruction was found in pieces of wood with little fouling attachment, whereas heavily fouled surfaces showed little or no wood destruction.

To investigate the possibility that fouling accumulation on a wood surface provides a natural barrier to wood-destroying organisms, the following experiment was carried out. Four pieces of cypress $2 \times 4 \times 18$ inches were fastened side by side at one end to a 1×2-inch cypress bar. The blocks were spaced ¾ inch apart. The unit of four blocks was suspended in the sea by a bronze chain. Two of the four blocks were wiped clean of fouling once a week, whereas the other two were allowed to accumulate fouling organisms. The blocks were immersed in Biscayne Bay at the Beach Boat Slips Corporation, Miami Beach, Florida, from October 16, 1944 to October 24, 1945.

Following the initial six months of exposure, one cleaned and one fouled block were removed from the sea and sectioned. Neither *Teredo* nor *Limnoria* was found in or on either of the blocks. This suggests the absence of these organisms from the waters during the period of exposure. The remaining blocks were removed and sectioned after a year of immersion. Their appearance following the year of exposure in the sea is shown in figure 1. The wood block cleaned periodically showed considerable *Teredo* attack inside and *Limnoria* destruction on the surface. In contrast, the heavily fouled surface showed no surface destruction by *Limnoria* and only one *Teredo* tube inside the block.

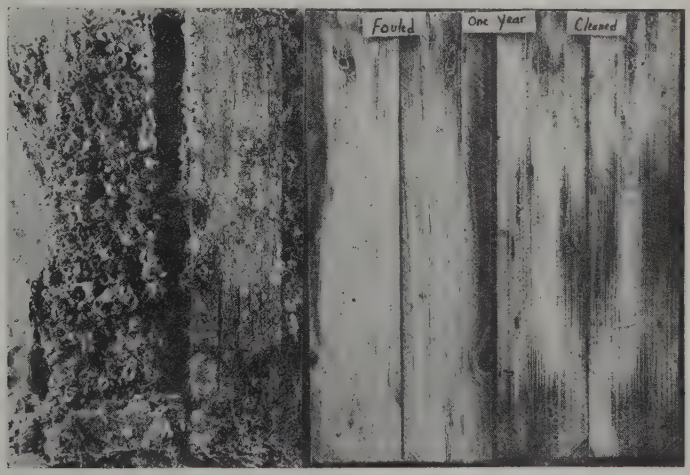

Fig. 1. The fouled and cleaned cypress blocks, following one year of immersion, are shown on the left. These same blocks, after sectioning, are shown on the right.

The single *Teredo* tube in the fouled block of wood was traced back into the suspension crossbar. The organism had apparently gained entrance into the wood through an area kept free of fouling by abrasion of the bronze chain.

It is evident from this demonstration that the natural accumulation of fouling organisms on a wood surface can effectively limit the depredations of such marine wood destroyers as *Teredo* and *Limnoria*.

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[1] Contribution No. 390 from the Woods Hole Oceanographic Institution.

Contribution No. 391

THE ZOOPLANKTON OF TISBURY GREAT POND

By

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VOLUME XII, ARTICLE 1

BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
Peabody Museum of Natural History
Yale University

Issued June, 1948
New Haven, Conn., U. S. A.

THE ZOOPLANKTON OF TISBURY GREAT POND[1]

By Georgiana Baxter Deevey[2]

Woods Hole Oceanographic Institution

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[1] Contribution No. 391 of the Woods Hole Oceanographic Institution, which provided funds for the cost of publication.

[2] Present address: Bingham Oceanographic Laboratory.

ABSTRACT

The purpose of this paper is to report the seasonal cycle of the zooplankton of Tisbury Great Pond and the effects of the wide range of temperature and salinity on the organisms. Zooplankton samples were taken usually at weekly intervals from May 20, 1945 to September 2, 1946. The majority of the samples were taken with a Clarke-Bumpus plankton sampler and a No. 10 net, but for a few only the net was used; since all the tows were made over the same course, quantitative estimates of the number of zooplankton per cubic meter have been made for the qualitative samples. The beach which separates the pond from the sea is opened at periodic intervals, so that during the year the salinity varies from less than 1 to 31‰ at the surface. The temperature varies from 0° to over 25° C.

The zooplankton is composed of several species of copepods, rotifers, *Podon polyphemoides*, larval forms of barnacles, gastropods, lamellibranchs, and polychaetes, and adventitious forms. *Acartia clausii* Giesbrecht was the dominant copepod during the first half of the year, disappearing at the beginning of July when the temperature reached 24° C. *Acartia tonsa* Dana appeared in June and was dominant throughout the summer. During both summers a sudden rise in salinity coincided with a marked decrease in numbers of this species. *Eurytemora hirundoides* (Nordquist) occurred during the period when *A. clausii* was dominant. These three species produced two generations a year in the pond. The rotifer *Synchaeta littoralis* Rousselet occurred erratically throughout the year, attaining its greatest maximum in May. The cladoceran *Podon polyphemoides* (Leuckart), which is extremely euryhaline but only moderately eurythermal, was present only during May and June while the temperature was rising from 12° to 24° C.

All the organisms living in the pond for any length of time are fairly euryhaline. The temperature is therefore more important in limiting the periods of their occurrence. The range of salinity bars the littoral forms that would occur in greater abundance if the pond were always open, as in estuarine situations. The members of the zooplankton are grouped according to the degree of their temperature and salinity tolerances.

Phytoplankton counts showed that diatoms were numerous throughout the year while flagellates and dinoflagellates were most abundant during the summer months. There were two pronounced maxima, a January diatom maximum and an August maximum of flagellates.

The total zooplankton counts showed a seasonal cycle with a single late spring maximum. Almost no zooplankton was present during the fall months; from January to March there was a barely perceptible increase in quantity, but from March to August the various species attained maximum numbers. There is no direct correlation between the abundance of the zooplankton and the temperature, the salinity, or the total numbers of phytoplankton.

INTRODUCTION

The primary objective of this paper is to report the seasonal changes in the zooplankton of Tisbury Great Pond. This is a shallow brackish water pond, separated from the sea by a narrow beach, on the southern

shore of Marthas Vineyard, Massachusetts. The salinity of the pond varies greatly, due to the periodic opening of the beach. This is done intentionally in order to maintain an adequate salinity for oyster culture. Because of this the pond presents a specialized type of environment, and it was of interest to discover what planktonic organisms are capable of surviving under these extreme conditions. During the year the temperature range is also considerable. Therefore, the secondary objective was to determine the effects of the wide variations of salinity and temperature on the zooplankton population.

Tisbury Great Pond differs from an estuary in that it is open to the sea for only limited periods of time. During these intervals littoral organisms, mainly copepods, enter the pond. Usually within a month's time the opening has filled with sand, so that the pond is once more cut off from tidal action. As the salinity decreases the adventitious forms that are unable to withstand the lower salinities disappear. Only euryhaline organisms are capable of living in the pond for any length of time. The zooplankton population consists, therefore, of brackish water species, neritic organisms, and the larval forms of adults adapted to these conditions.

The zooplankton tows were made by Willard Huntington as part of the collection of samples and data for the Woods Hole Oceanographic Institution project concerned with the study of salt ponds under the direction of George L. Clarke. This was a cooperative investigation. The results of the analysis of the oysters will be published later by Yvette H. Edmondson. Phytoplankton counts, covering the twelve month period from September 1945 to September 1946, were made by Mary Goffin. This material will not be published separately, and therefore a brief summary of the phytoplankton is included in this paper in order to complete the picture of the plankton and to compare the seasonal abundance of the phytoplankton and the zooplankton.

ACKNOWLEDGMENTS

I am indebted to George L. Clarke for suggesting this problem, for the privilege of examining this material, and for making it possible for me to carry out the work at the Woods Hole Oceanographic Institution and later at the Bingham Oceanographic Laboratory. Grateful acknowledgment is also due to my co-workers, especially to Y. H. Edmondson for sharing with me the data for temperature, salinity, and

phytoplankton and to W. T. Edmondson for the identification of the rotifers. I am extremely grateful to Daniel Merriman, Director of the Bingham Oceanographic Laboratory, for granting me the facilities of the laboratory. For their advice and very helpful criticism of the manuscript, I am indebted to Ernest F. Thompson, G. L. Clarke, and my husband, Edward S. Deevey, Jr.

METHODS

The Clarke-Bumpus plankton sampler (Clarke and Bumpus, 1940) was used in making the zooplankton tows. These were taken usually at weekly intervals from May 20, 1945 to September 2, 1946. The tows were made in the vicinity of the oyster beds between two landmarks on the southwestern shore of the pond. The first several tows were made with a No. 2 silk net, but from June 18, 1945 onward a No. 10 silk net was used. Few samples could be obtained in midwinter as the pond was frozen over for part of December, January, and February. The quantitative data cover the period from August 31 to December 2, 1945; then there was a long break in midwinter, and although samples were obtained on January 6 and February 10, 1946, unfortunately the number of revolutions was not recorded. The quantitative data continue from March 10 to July 7, 1946, when the sampler was returned to Woods Hole. The remaining 1946 summer samples were taken with a No. 10 net. Since all the tows were made over the same course, quantitative estimates for the qualitative samples have been obtained by averaging the number of revolutions recorded for the quantitative samples. The average number of revolutions, 328.2, and its standard deviation of 165.5, provide a quantitative "belt of confidence" for the qualitative samples. From this the approximate number of organisms per cubic meter can be estimated.

One to four counts were made on each sample, the number depending largely on the quantity and variety of organisms present. As a rule at least 500 organisms were counted, except in the case of the extremely scanty fall samples, where on one occasion, for example, 40 per cent of the total sample yielded only 36 organisms.

It has been impossible to identify the copepod nauplii while making the counts. In the later sections, where the developmental stages of the most important copepods are considered, the nauplii are assumed to belong to the currently dominant species. There can be little doubt

of the identity of the great majority of nauplii in each case since only one species was abundant at any one time.

SALINITY AND TEMPERATURE

Fig. 1 gives the temperature and salinity data for the period covered by the samples. These data are for the surface temperatures and salinities only, since the tows were made just below the surface. Hydrometer readings were made whenever samples were collected and these have been converted to salinity readings by means of Knudsen's tables. The times when the beach was opened are indicated by arrows in Fig. 1; in 1945 this occurred on May 17, August 12–13, and December 10, and in 1946 on March 11, in late June and in late August. The extreme range of salinity at the surface during the period studied is from less than 1 to 31°/₀₀. The salinity varied from the surface to the bottom at around eight or nine feet, the lower layers always being more saline. The water was mixed when the beach was opened; as the pond closed the less saline water was found at the surface. Extreme differences in salinity resulted in mid-December when the pond was frozen and the beach was opened; at five feet the salinity was 26.05°/₀₀, while the surface layer was fresh.

The temperature cycle of the pond showed a range of from 0° to over 25° C. at the surface. From December through February the temperature varied between 0° and 6° C.; during March and April a slow rise occurred, followed by an abrupt increase in May. By late June the temperature reached 24° C. and until mid-September it oscillated between 20° and 25° C. Early in October the temperature dropped rapidly, then continued to decrease more slowly to the minimum. Only slight thermal stratification occurred.

THE SEASONAL CYCLE OF THE ZOOPLANKTON

The zooplankton of Tisbury Great Pond is composed of the following elements: (1) The copepod population, of which *Acartia* is the dominant genus. (2) Sporadic maxima of larval forms, which include barnacle nauplii and cyprids, gastropod and lamellibranch veligers, and polychaete larvae. (3) A rotifer population, consisting of two species of *Synchaeta*. (4) A late spring population of the cladoceran *Podon polyphemoides*. (5) Forms entering the pond accidentally when the beach was opened. Of these *Sagitta* appeared in greatest quantity

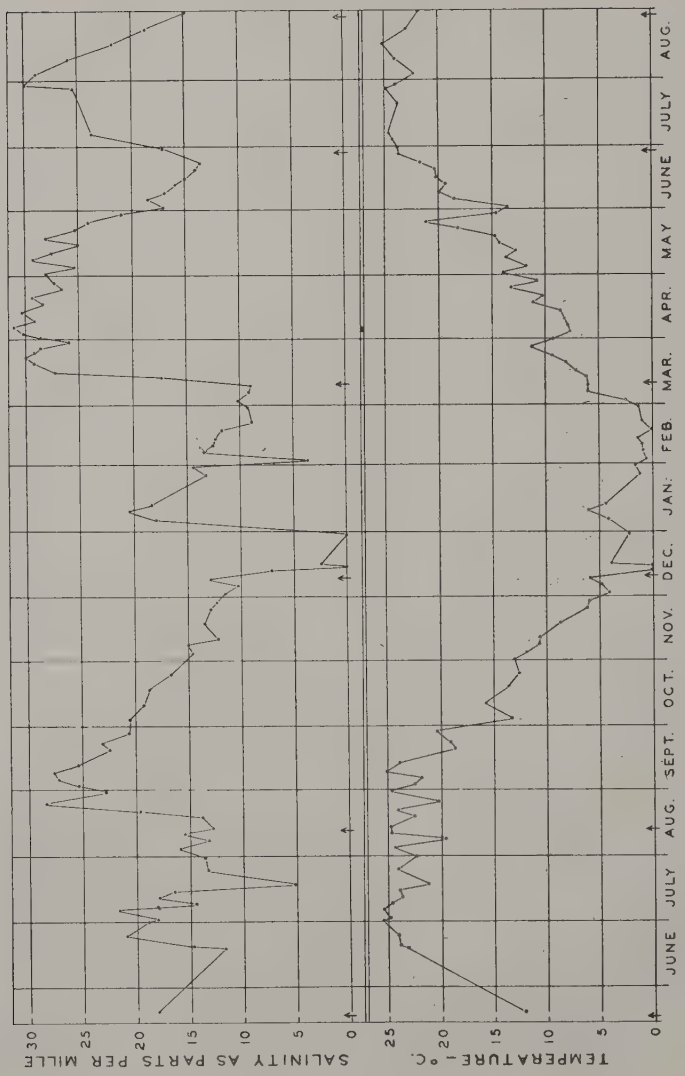

Figure 1. The temperature and salinity of the surface layers of Tisbury Great Pond from May 20, 1945 to September 2, 1946.

TABLE 1. Seasonal Cycle of Abundance of the Major Elements of the Zooplankton of Tisbury Great Pond. Semiquantitative, as Number per Cubic Meter. x: 1–100; xx: 101–1,000; xxx: 1,001–10,000; xxxx: 10,001–100,000; xxxxx: 100,001–1,000,000.

	1945							1946							
	June	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Acartia clausii	xxx	x	—	—	x	x	—	x	x	xx	xxx	xxxx	xxxx	xx	—
Acartia tonsa	xxxx	xxxx	xxxx	xx	—	—	—	x	—	—	—	—	x	xxx	xxx
Eurytemora hirundoides	xx	x	—	—	—	x	—	xx	xx	xxx	xx	xx	xx	x	—
Centropages hamatus	x	x	—	—	—	—	—	x	x	x	x	x	x	x	—
Oithona brevicornis	—	—	—	—	—	—	—	—	—	x	x	x	xx	xx	xx
Harpacticoids	x	x	x	x	x	x	—	x	—	xx	xx	x	xx	xx	x
Copepod Nauplii	xxx	xxxx	xxxx	xxx	xx	xx	x	xx	xx	xxxx	xxx	xxxx	xxxx	xxxx	xxx
Podon polyphemoides	xxx	—	—	—	—	—	—	—	—	—	—	xxx	xxx	—	—
Barnacle larvae	x	x	x	x	—	x	x	x	x	x	xx	xxx	xxx	x	x
Polychaete larvae	xx	x	xx	xx	x	xx	x	—	x	x	xxxx	xxxx	xx	xx	xx
Gastropod veligers	xxx	x	x	xx	xx	x	—	—	x	x	x	xxx	xxxx	xxx	xx
Lamellibranch veligers	x	xxx	xx	xx	xx	xxx	xx	—	—	—	x	xxx	xxx	xxx	xx
Synchaeta littoralis	—	—	x	xx	—	—	x	xx	xxx	xxx	xxx	xxxxx	xxx	xx	x
Synchaeta sp.	—	—	—	—	—	xx	xx	x	x	—	—	—	—	—	—
Aver. Surface Temperature (° C.)	—	23.9	22.9	21.6	14.15	9.9	2.97	3.46	0.91	7.33	9.72	15.0	20.1	24.3	23.8
Surface Salinity Range (°/oo)	11.7–21.9	5.2–21.6	12.8–28.4	20.5–27.6	16.7–20.5	12.2–15.0	0–12.8	13.2–20.3	3.6–13.3	9.0–29.9	26.7–31.0	25.0–29.2	13.7–18.4	17.0–29.8	18.5–28.9

on one occasion, but several littoral copepods also belong in this category. Table I summarizes, semiquantitatively, the seasonal abundance of the various organisms and also gives the average monthly surface temperature and the surface salinity range in parts per mille.

The Copepod Population

Acartia tonsa Dana

Appeared in mid-June 1945, late June 1946
Disappeared in September
Temperature range: 19.6°–25.4° C.
Extreme salinities from both summers: 5.2–29.8°/₀₀

Acartia tonsa is the most abundant copepod in Tisbury Great Pond during the summer months. This is a littoral form capable of living in waters of relatively low salinities. In Chesapeake Bay, Davis (1944) found it in water with a chlorinity of 0.4°/₀₀ as well as in water with a chlorinity approaching that of the ocean. Bigelow and Sears (1939) considered it probably an indicator of coast water. Cape Cod forms the northern boundary of this species (Bigelow, 1926). It is abundant in the Woods Hole region, both in brackish ponds and in the open water off Marthas Vineyard (Wilson, 1932a; Sharpe, 1910; Clarke and Zinn, 1937). *Acartia tonsa* has also been reported abundant in the

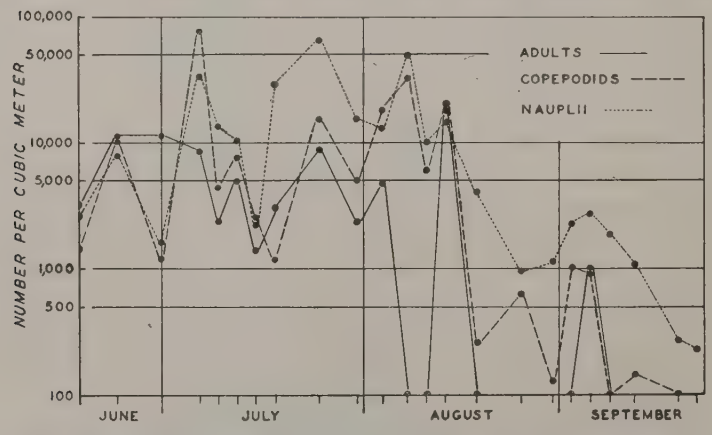

Figure 2. The estimated number per cubic meter, plotted on a logarithmic scale, of nauplii, immature copepodids, and adults of *Acartia tonsa* for the summer of 1945.

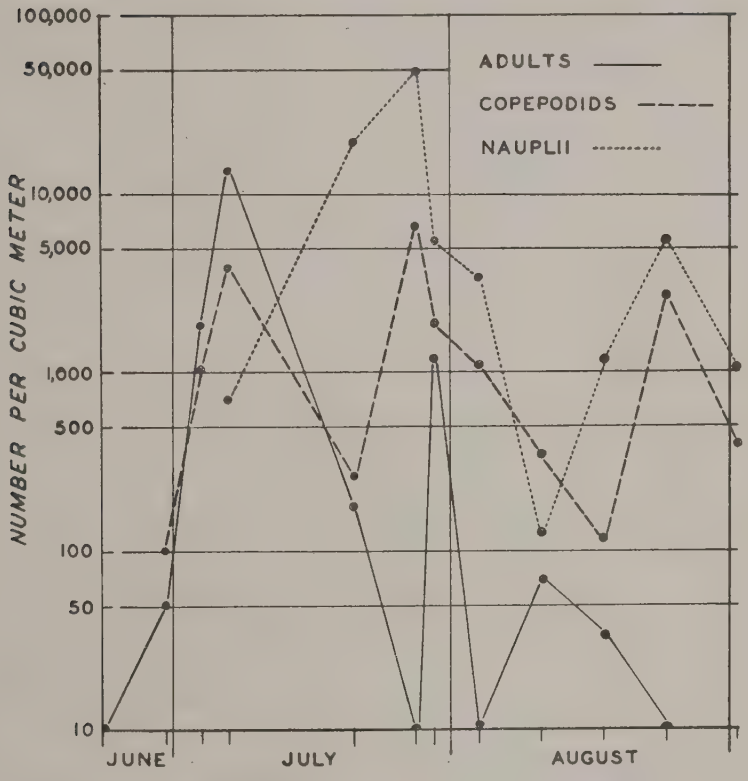

Figure 3. The estimated number per cubic meter, plotted on a logarithmic scale, of nauplii, immature copepodids, and adults of *Acartia tonsa* for the summer of 1946.

bays in San Diego, California by Esterly (1905), from the Louisiana coast by Foster (1904), and from Long Island bays (Tressler and Bere, 1939). Fish (1925) listed *A. tonsa* as one of the two most typical summer copepods in Woods Hole Harbor.

Figs. 2 and 3 give in graphical form the estimated numbers per cubic meter, plotted on a logarithmic scale, of nauplii, copepodids, and adults of *Acartia tonsa* for the summers of 1945 and 1946 in Tisbury Great Pond. In Fig. 2, two major maxima of adults are apparent, one in late June to early July and the other in mid-August. Each of these was

followed by a secondary maximum, one in late July and the other in early September. Bursts of nauplii produced by the adults were evident throughout July and early August. Immediately following the mid-August adult maximum, however, there was a sudden drastic reduction in numbers of the *Acartia* population. The total number of all stages from nauplius to adult dropped from 55,000 on August 14 to about 4,000 per cubic meter on August 19. Nauplii were not produced in any quantity by the adults maturing in mid-August, and after the small peak of adults in early September, mature *Acartia tonsa* disappeared from the samples. Copepodids remained in small numbers until early October, and a few adult females were observed in early January 1946, but no more *A. tonsa* were found until the following June.

During the summer of 1946 (see Fig. 3), *A. tonsa* was not as successful as in 1945. The first adult maximum occurred in early July and was followed by a peak of nauplii and then a secondary adult maximum in late July, but between July 28–30 there was, once again, a sharp drop in numbers of the total *Acartia* population, including adults, copepodids, and nauplii, from 55,000 to a little over 8,000 per cubic meter. The latter number was not exceeded for the rest of the summer, nor did the second major maximum of adults materialize in the samples, although the small numbers of adults found in mid-August may represent the survivors of this group. It is possible, also, that a maximum of adults may have occurred in September, but the data stopped on September 2 and on that day the stock of *A. tonsa* was very low in numbers.

The cause of the abrupt decimation of the *A. tonsa* population is not clearly apparent, but on both occasions the marked diminution in numbers coincided with a sudden increase in the salinity. Fig. 4 shows in graphical form on a logarithmic scale the total numbers of copepodids and adults plotted together with the surface salinity readings for the summer of 1945; the arrow indicates the date the beach was opened. In this case the total numbers of copepodids and adults dropped from about 40,000 on August 14 to 250 per cubic meter on August 19. The beach was opened on August 12–13, but there was a time lag before the change in salinity showed up in the hydrometer readings. According to the readings, the salinity on August 19 was 14.0°/₀₀, and the drastic rise in salinity occurred between then and August 22, with the maximum salinity of 28.5°/₀₀ on August 26. Un-

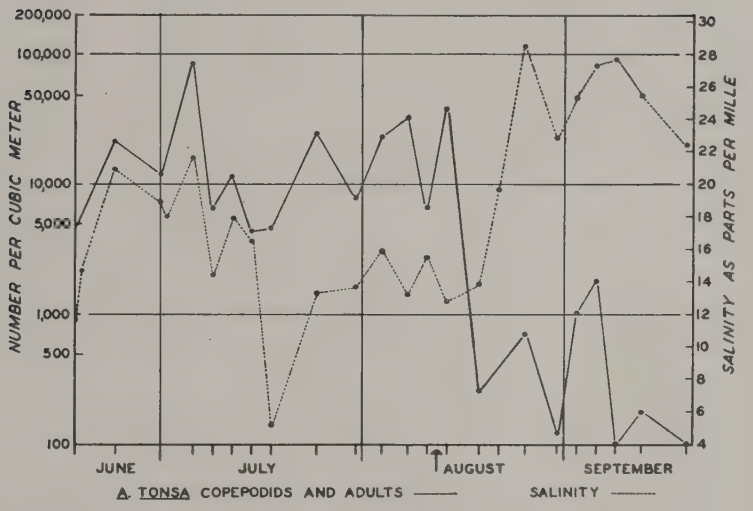

Figure 4. The total number per cubic meter, on a logarithmic scale, of copepodids and adults of *Acartia tonsa* plotted with the surface salinity for the summer of 1945.

questionably the salinity at the deeper levels was much greater than at the surface. It is also probable that the *Acartia* came in contact with a layer of this much more saline water before the hydrometer registered the change at the surface and that this may have been the cause of the drastic reduction in numbers of the population. As an alternative it is perhaps possible that tidal currents may have dispersed the population on this occasion, but this would not apply to the 1946 decrease.

In 1946 the circumstances were different. Fig. 5 gives in graphical form on a logarithmic scale the total numbers of adults and copepodids plotted with the surface salinity. In 1946 fewer numbers of adults and copepodids were found, and so the total numbers of *Acartia* of all stages including nauplii are also shown. During this summer the beach was opened at the end of June and again at the end of August, as indicated by arrows in Fig. 5. In this case *A. tonsa* appeared immediately after the opening of the beach at the end of June. The salinity had been rising from 13.5°/₀₀ in the latter part of June to 25.5°/₀₀ on July 28. During the next two days, within which time the marked decrease in total numbers of *Acartia* occurred, the salinity rose

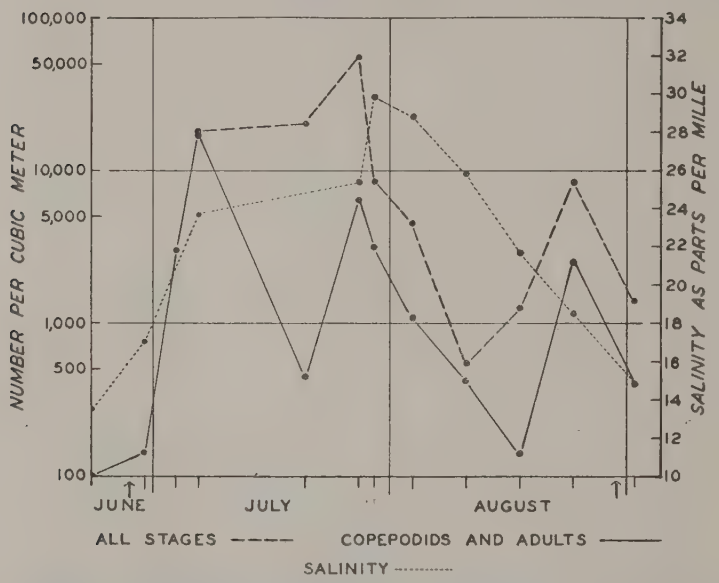

Figure 5. The total number per cubic meter, on a logarithmic scale, of all stages and of copepodids and adults of *Acartia tonsa* plotted with the surface salinity for the summer of 1946.

to 29.85°/₀₀. It is impossible to prove from these data whether this increase is sufficiently abrupt to cause such a sudden drop in numbers of *Acartia*. If these changes in salinity are concerned in the equally drastic diminution of the *A. tonsa* population, it is apparent that only the most abrupt increases at the higher salinity levels can be responsible. A steep drop in salinity in 1945 (see Fig. 4) did not affect the numbers of *Acartia*, nor did sharp rises in salinity which occurred over a week's time. However, the coincidence of an abrupt rise in salinity with a drastic reduction in numbers of *Acartia tonsa*, occurring twice, seems too great to be fortuitous. The evidence indicates that although *A. tonsa* has a wide salinity tolerance it may not be sufficiently heteroeuryhaline to withstand a sudden change in salinity.

In 1946, due to the fact that *A. tonsa* was found in numbers only during the month of July, adults of the midsummer maximum did not appear in appreciable quantity, but in 1945 two months elapsed before

the sudden mortality of *Acartia* occurred. Judging from the data for this latter period (see Fig. 2), *A. tonsa* produced one generation during the summer. During the period studied, two generations a year were produced, the first maturing in late June and early July and the second in mid-August. The length of time intervening between the two major maxima of adults was six to seven weeks in summer, from late June-early July to mid-August. A similar interval occurred between the two secondary adult maxima in late July and early September; the late July group probably represents a second brood of the parents of the early July maximum. Six to seven weeks is a reasonable time interval for the development of *Acartia* at temperatures ranging between 20° and 25° C., and is within the time range obtained for other calanoid copepods. The developmental period of *Calanus finmarchicus* varies considerably, with temperature as an important factor, from one month in the laboratory (Nicholls, 1933) to three months in the Norwegian Sea (Ruud, 1929). In the Gulf of Maine 2½ months are necessary for its development from egg to spawning adult (Fish, 1936a). Clarke and Zinn (1937) also gave 2½ months as the approximate interval between the spring and summer generations of *Calanus* off Marthas Vineyard. *Pseudocalanus minutus* has a developmental period of approximately two months in the Gulf of Maine (Fish, 1936b). It is a fair assumption that no more than six or seven weeks should be required for the development of *A. tonsa* under summer conditions.

Less can be said conclusively about the origin and development of the generation reaching maturity in late June and early July. It is not inconceivable, since such is apparently the case with *Calanus*, that offspring of the August maximum overwinter in late copepodid stages to form the first generation the following year. But we lose sight of *A. tonsa* until it appears in numbers in late June. During the spring, however, immature stages may have been overlooked, due to the presence in numbers of *A. clausii*. It is also possible that *A. tonsa* may not have overwintered in the pond from 1945 to 1946, and that this species returned after the opening of the beach late in June 1946. On the other hand, in the spring of 1945 *A. tonsa* did not appear until about a month after the beach was opened in May.

Acartia clausii Giesbrecht

Appeared in early copepodid stages in October
Disappeared in early July
Maxima in mid-April and June
Temperature range: 0°–24° C.
Extreme salinities: less than 1–31°/₀₀

Acartia clausii is a northern species and has a lower temperature range than *A. tonsa*. From Cape Cod south it is strictly neritic (Bigelow and Sears, 1939), but in more northern waters it occurs farther out from the coast. It is widespread over the Gulf of Maine, although more numerous in shallow waters (Bigelow, 1926). In reporting the Port Erin plankton investigations, Johnstone, Scott and Chadwick (1924) listed *A. clausii* as a North Atlantic oceanic species. Wiborg (1940), in his study of the zooplankton of Oslo Fjord, also considered it dependent on Atlantic water to a certain extent. On the other hand, Gurney (1928–1929) referred to *A. clausii* as a littoral and brackish water form. It was found to be the dominant species in l'Etang de Thau, a pond connected with the Mediterranean (Fatemi, 1938) and also in the Thames estuary (Wells, 1938). In 1932 Wilson (1932b) reported it the dominant copepod in Chesapeake Bay throughout the year. More recently Davis (1944) found *A. tonsa* more numerous than *A. clausii* in the Bay, although Wilson had not found *A. tonsa* there. Davis was not specific about the dates when his samples were collected, but he said that most of them were obtained in August 1942, and some at other times, especially during the winter months of 1942–1943. From this it is impossible to tell whether the greater abundance of *A. tonsa* is seasonal, or whether *A. tonsa* is now the dominant form during the entire year. In any event, *A. tonsa* has only recently appeared in Chesapeake Bay to equal or exceed *A. clausii* in numbers.

From October to March only a few *Acartia clausii* were found in Tisbury Great Pond. During the fall months, small numbers of early copepodid stages were observed. Specimens examined from a late November sample proved to be at Stages III and V as described by Grandori (1912). By early January 1946 a few adults were also present. From then until late March *A. clausii* was well outnumbered by rotifers and *Eurytemora hirundoides*, the only organisms to increase in numbers during the early months of the year.

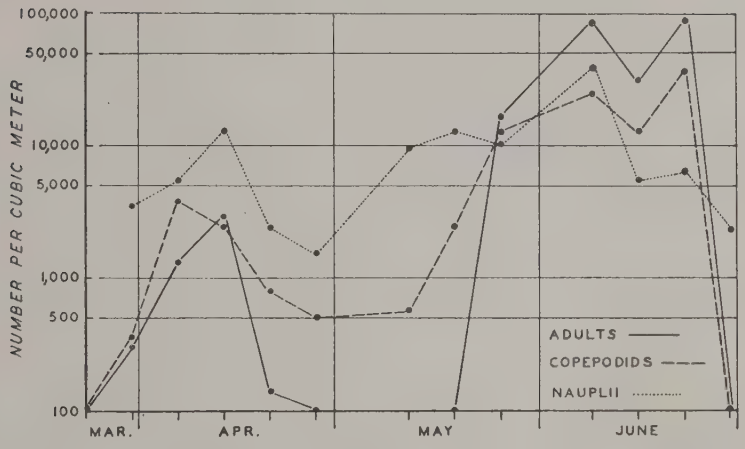

Figure 6. The number per cubic meter, on a logarithmic scale, of nauplii, copepodids, and adults of *Acartia clausii* for the spring of 1946.

Fig. 6 gives in graphical form, plotted on a logarithmic scale, the age structure of the *Acartia clausii* population during the period from late March to the end of June. Two maxima of adults were apparent, the first in mid-April and the second in June. The first spring generation consisted of relatively small numbers, only about 3,000 adults per cubic meter, compared with the later June generation. This may be partly due to the predatory activities of the hydromedusae and sagittae that were present in the pond during April. Fatemi (1938) also noticed a decrease in the number of *Acartia* coincident with the presence of hydromedusae. *A. clausii* was most abundant throughout June, but a week before its disappearance the highest count of 86,000 adults per cubic meter was obtained. About 122,000 *Acartia* per cubic meter, including immature copepodids and adults, virtually disappeared in a week's time. Between June 23 and June 30, when the samples were taken, the beach was opened again, but this cannot be entirely responsible for the disappearance of the *Acartia clausii* population, since *A. clausii* vanished on July 2 the previous summer, although the beach was not opened at that time. In 1946 a few adult *A. clausii* were present until July 4.

In this instance the evidence indicates that temperature was the deciding factor, limiting the period of occurrence of *A. clausii* in the

surface layers of Tisbury Great Pond. During the early spring an abrupt rise in salinity from 9.0 to 29.9°/₀₀ did not have an adverse effect on this species. At the time of the April maximum the temperature was 8.6° C., and the salinity was 30.3°/₀₀. In June, while *A. clausii* was present in large numbers, the temperature varied between 20° and 21.7° C., and the salinity between 13.5 and 20°/₀₀. It is evident that *Acartia clausii* has a wide temperature and salinity tolerance. However, temperatures approaching and exceeding 24° C. may have a deleterious effect on the population. Both in 1945 and in 1946 the temperature had reached this point when *Acartia clausii* disappeared.

A. clausii had two generations during the year. The time interval between the mid-April maximum and the June maximum is eight to ten weeks, and therefore this is the length of time required for the spawning and development of the late spring generation. As in the case of the first generation of *A. tonsa*, the origin and the length of the developmental period of the first generation of *A. clausii* are not fully evident in these data, but the appearance of young copepodids in the fall suggests that a few offspring of the June maximum may have survived the summer, perhaps at or near the bottom of the pond. A slow development of these individuals is also indicated. If these copepodids are the offspring of the previous June maximum, the length of the developmental period was about ten months at most. The present data do not offer sufficient evidence to prove whether young stages of *A. clausii* and *A. tonsa* survive periods of adverse conditions in small numbers, or where this may occur. However, this cyclic alternation of *A. clausii* during the spring months and *A. tonsa* during the summer, observed for two successive spring and summer seasons, is probably a yearly occurrence in Tisbury Great Pond, at least under present conditions. If the pond were allowed to remain closed for an extended period it would be interesting to learn how long each population could maintain itself at extremely low salinities.

Eurytemora hirundoides (Nordquist)

Appeared in early copepodid stages in November
Disappeared in early July
Temperature range: 0°–24° C.
Extreme salinities: less than 1–31°/₀₀

E. hirundoides is common in brackish and fresh ponds in the Woods Hole area, although it occasionally appears in waters of higher salinity.

Fish (1925) reported its occurrence in Woods Hole harbor during the spring months, and Davis (1943) found it in Chesapeake Bay under widely varying conditions of temperature and salinity. It is scarce in the Thames estuary (Wells, 1938) and in Oslo Fjord (Wiborg, 1940), although Sars (1903) found it in both brackish and salt water on the Norwegian coast. That it is predominantly a brackish water form is evidenced by the fact that it was not taken by Bigelow (1926) in the Gulf of Maine or by Bigelow and Sears (1939) in their study of the coastal waters from Cape Cod to Cape Hatteras.

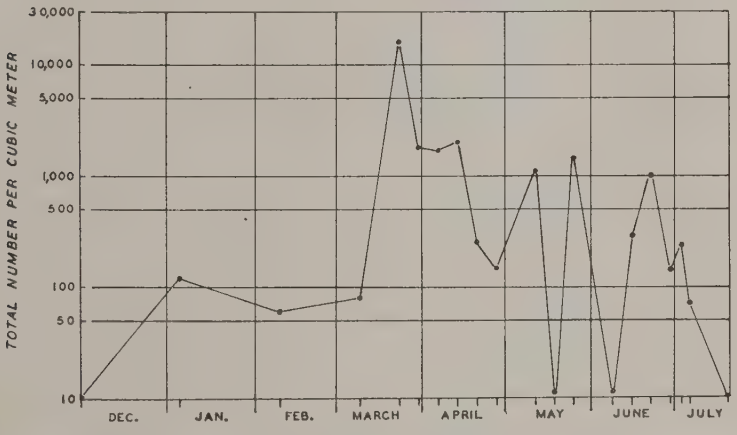

Figure 7. The total number per cubic meter, on a logarithmic scale, of copepodids and adults of *Eurytemora hirundoides* from January to July 1946.

Considering its salinity preferences it is surprising that *E. hirundoides* is not a more dominant form in Tisbury Great Pond. Possibly the sudden increases in salinity when the beach is opened have an adverse effect on it, but this is not borne out by the data, for the largest number recorded, nearly 17,000 per cubic meter, occurred coincident with a sharp rise in salinity from 9 to 30‰. Another possibility is that *Acartia clausii* and the other organisms abundant during the spring months may offer too much competition.

E. hirundoides was found in the pond throughout the period during which *A. clausii* was present, but it was much less abundant than *Acartia* except for the early months of the year. Fig. 7 gives in graphi-

cal form the total number of adults and copepodids of *Eurytemora* per cubic meter, plotted on a logarithmic scale, for the period of its occurrence. In early January 1946, copepodid stages II to V were present. In early March adults began to appear, and by late March many young copepodids at stages I to III were also observed. Thereafter the numbers declined rapidly as *Acartia clausii* increased in abundance. During the first half of April adults and maturing copepodids were predominant, but throughout the latter half of this month and during May a succession of copepodid stages occurred. The later stages of development passed through during early June culminated in a maximum of adults shortly before the end of this month. In mid-June 1945 *E. hirundoides* attained a similar maximum of adults. Adults continued to occur until early July in 1945 and in 1946 and then, like *Acartia clausii*, *Eurytemora hirundoides* vanished from the samples.

The data show that in Tisbury Great Pond *E. hirundoides* produced two generations a year synchronous with those of *Acartia clausii*, which it so closely paralleled in period of occurrence. The reproductive activity of the early generation extended from early March to early April, while the adults of the June maximum produced no offspring that were immediately apparent in the samples. The length of time necessary for the development of the June generation was approximately 2½ months. As in the case of *Acartia clausii*, the higher summer temperatures must be responsible for the disappearance of *Eurytemora hirundoides* early in July.

Size Range of the Generations of *Acartia* and *Eurytemora*

It has been noted, especially with regard to *Calanus finmarchicus*, that the size range of the several generations produced throughout the the year varies. Bogorov (1934) and Marshall, Nicholls, and Orr (1934), for example, found that the largest adults of *Calanus* appeared in the spring generation that was spawned at the lowest temperatures. The greater size was not correlated with the length of the developmental period. On the other hand, Clarke and Zinn (1937) reported that the *Calanus* spawned in June and maturing the following January and February were larger than those developing during the early months of the year. An intensive study of the variation in size of *A. tonsa*, *A. clausii*, and *E. hirundoides* has not been made, but random measurements of males and females from the two generations of each species indicate that the adults of the first generation attained a slightly

larger size than their offspring of the second generation. In Table II the length range of individuals of each generation of the three species is tabulated; the length range of each species as given by Wilson (1932a) is included for comparison. Approximately 50 specimens of *E. hirundoides* and 300 specimens of each species of *Acartia* were measured. In the case of these three species the individuals developing at lower temperatures and at a slow rate attained slightly greater size. It is also of interest to note that some individuals of *E. hirundoides*, a brackish water form, were larger than the maximum recorded by Wilson, while the majority of the specimens of *Acartia* that were measured were below the minimum recorded length.

TABLE II. Variation in Length, in Millimeters, between Individuals of the First and Second Generations of *Acartia clausii*, *A. tonsa*, and *Eurytemora hirundoides*

	A. clausii	*A. tonsa*	*E. hirundoides*
First Generation			
Female	1.0–1.2	0.95–1.2	1.1–1.4
Male	0.9–1.05	0.85–1.0	0.9–1.25
Second Generation			
Female	0.9–1.1	0.85–1.0	0.9–1.1
Male	0.8–1.0	0.80–0.9	0.8–0.95
Reported Length (Wilson, 1932a)			
Female	1.15–1.25	1.25–1.5	1.0–1.25
Male	1.0–1.1	1.0–1.15	0.9–1.0

Oithona brevicornis Giesbrecht

Extreme salinities: 13.5–31°/₀₀

Oithona brevicornis is the only cyclopoid copepod that was found in any numbers in Tisbury Great Pond. During the period studied it entered the pond and became established there. It first appeared during the latter part of March 1946, shortly after the beach was opened, and was present until the end of the observations in early September. The total numbers of *O. brevicornis* per cubic meter for this period are shown in graphical form in Fig. 8. A small maximum in April was followed by a much higher peak in June. Two smaller maxima occurred in late July and late August. Females with egg sacs were observed in April, June, late July, and late August to early September. This indicates, but does not prove, four generations during this time, with a two month interval as the developmental period

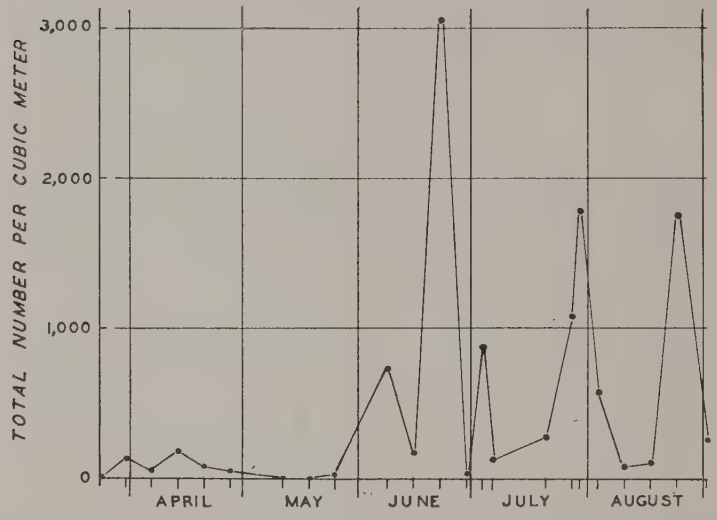

Figure 8. The total number per cubic meter of *Oithona brevicornis* from April through August 1946.

for the June maximum, while the last two generations were about a month apart.

Oithona brevicornis is an exceptionally small copepod, males and females averaging around 0.5 mm. in length, although occasional females 0.6 mm. long were encountered. Nearly all the individuals counted were adults, none smaller than 0.4 mm. in length being observed. A month is probably not too short a time for the development of this species in summer at temperatures ranging between 22° and 25° C., since Fish (1936c) gave six weeks as the interval between generations of *Oithona similis*, a larger species, during the summer in the Gulf of Maine.

Due to the fact that *Oithona brevicornis* did not become a member of the pond fauna until relatively late in the period under investigation, it would be misleading to give the known dates of its occurrence as limiting its seasonal appearance. The known temperature range, 7.7° to 25.2° C., also cannot represent the true limits of its tolerance. However, this species has withstood variations in salinity from 13.5 to 31‰. Wilson (1932b) also reported a wide salinity range for *Oithona*

brevicornis in Chesapeake Bay, where the average salinity was less than 10°/₀₀ at some of the stations where it was found. *O. brevicornis* was widely distributed throughout the Bay during the entire year and ranked third in abundance after the two species of *Acartia, A. clausii* and *A. longiremus*. *O. brevicornis* is apparently both a neritic and a brackish water species.

Other Copepods

The copepods included under this heading are only those which may be considered as living in the pond. The adventitious species are listed with other accidental visitors. *Centropages hamatus* is the only other calanoid copepod that was found for an extended period of time. This is a littoral species that penetrates estuarine situations. It has been reported from the Thames estuary (Wells, 1938), from the Norfolk estuaries (Gurney, 1928–1929), and from the brackish pond connected with the Mediterranean that was studied by Fatemi (1938). In Oslo Fjord *C. hamatus* is the most important copepod in the innermost part of the fjord, occurring in maximum numbers in summer (Wiborg, 1940). It is characteristic of winter plankton in Woods Hole harbor (Fish, 1925) but has been found most abundant in June and July off Marthas Vineyard (Clarke and Zinn, 1937).

Centropages hamatus first appeared in early January 1946 and occurred fairly consistently in small numbers until early July. A small maximum was found in April, while another was observed in early July. During the period of its occurrence it experienced the same range of temperature and salinity as *Acartia clausii* and *Eurytemora hirundoides*. That it remained for so long a period is proof of its ability to withstand greatly varying salinities and temperatures.

It is questionable whether *Paracalanus crassirostris* Dahl should be considered a member of the pond fauna or an adventitious form. It was found in the samples during the latter half of March, most of April, and in August, 1946. However, it is of interest to note its presence, since this species is not listed by Wilson (1932a) and may not have been reported from this region before. Its relative, *Paracalanus parvus*, has been recorded from the Gulf of Maine to Chesapeake Bay. *P. crassirostris* is reputedly the smallest calanoid, adult females measuring about 0.5 mm. in length, and this may be one reason why it has not been observed. Davis (1944) has described *Paracalanus crassirostris* Dahl var. *nudus* Davis from Chesapeake Bay. His specimens

differed from all descriptions of *P. crassirostris* in having a less well developed spiny armature on the rami of the swimming legs, the second legs being entirely bare. The specimens of *P. crassirostris* found in Tisbury Great Pond agree in all respects with Gurney's (1927) description of this species from specimens obtained from the Suez Canal, and therefore are not similar to the variation of this species described by Davis. Only adult females were found in Tisbury Great Pond.

Aside from *Oithona brevicornis*, two other species of cyclopoid copepods were found in the pond. *Halicyclops magniceps* (Lilljeborg) is definitely a brackish water form (Gurney, 1928–1929), which occurred sporadically throughout the year, with maximum numbers in late June. Females with egg sacs were observed in June, July, and August, immature stages in September and November, and females in January. In late June and early July 1946, males, females, and immature stages were present.

One male specimen of *Myicola major* (Williams) was found in the plankton in late July 1945. This record is of interest, since, according to Wilson (1932a), this species has heretofore been found only in the mantle cavities of *Mya arenaria*, *Venus mercenaria*, and *Mactra solidissima* in Narragansett Bay.

A number of harpacticoid copepods, not all of which have been identified, occur in Tisbury Great Pond. Table III lists the species and the known times of their occurrence. Many of these undoubtedly were present at other times, but since it was always necessary to dissect most of these species in order to identify them a complete study has not been made. *Tachidius brevicornis* Lilljeborg, a brackish water species, and *Harpacticus tenellus* Sars were the harpacticoids noted most frequently. *T. brevicornis* was most abundant during the spring, while *H. tenellus* was fairly common especially during the summer months. *Parategastes sphaericus* (Claus) is strikingly different in appearance from other harpacticoids, and therefore it is certain that this species occurred only during July and August of both summers. Fish (1925) also found this a common summer form in Woods Hole harbor.

TABLE III. KNOWN TIMES OF OCCURRENCE OF HARPACTICOIDS IN TISBURY GREAT POND

	1945							1946						
	June	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Tachidius brevicornis	x	x	—	—	—	x	—	x	—	x	x	x	—	—	—
Harpacticus tenellus	—	x	x	x	—	x	—	x	—	x	—	x	x	x	x
Paralegastes sphaericus	—	x	x	—	—	—	—	—	—	—	—	—	—	x	x
Echinosoma curticorne	—	—	—	—	—	—	—	x	—	—	x	—	—	—	—
Dactylopusia brevicornis	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
Dactylopusia vulgaris	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
Microsetella norvegica	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—
Amphiascus pallidus	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—
Mesochra pygmaea	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—

Larval Forms

Barnacle Nauplii and Cyprids

Balanus balanoides: March–April
Balanus crenatus: latter half of April–early July
Balanus eburneus (?): late July–September 1946; November, 1945

Adult barnacles apparently do not occur in abundance in the vicinity where the plankton tows were made, since neither nauplii nor cyprids were taken in any great quantity. According to Fish (1925), identification of the nauplii of the species found in the Woods Hole region is facilitated by the fact that they have different breeding periods: *Balanus balanoides* larvae occur from December to April, *B. crenatus* larvae in July, and *B. eburneus* larvae from August to October. He found *Chthamalus stellatus* larvae in late July or early August, within the period for *B. eburneus.*

The identification of acorn barnacle nauplii would not be difficult were it not for the paucity of published accounts of the developmental stages of the various species. The naupliar stages of *B. crenatus* have been studied by Herz (1933), while those of *B. balanoides, Chthamalus stellatus,* and *Verruca stroemia* have been worked out by Bassindale (1936). These papers serve to emphasize the differences between the various species in shape, size, and relative proportions, as well as in the setation of the antennules, antennae, and mandibles. However, judging from the Tisbury Great Pond material, variations in the size and setation of *B. balanoides* nauplii are slightly greater than Bassindale found them to be.

Nauplii and cyprids of *Balanus balanoides* were found from late March to the end of April but were most abundant during the first half of April. The larger nauplii were intermediate in size and setation between two of Bassindale's stages. This would be expected if the number of instars is not fixed. The length of the cyprid varied considerably also, from 0.8 to 1.25 mm., although the majority agreed closely with Bassindale's figure of 0.94 mm. This variation in the size of the cyprid gives evidence of a range in size and possibly in number of instars of the naupliar stages.

Balanus crenatus nauplii appeared during the latter half of April and were present until the end of June. Cyprids were first found during the second week of May and continued to appear until early July. The nauplii of *B. crenatus* occurred in greater numbers than those of

the other species. Two maxima of nauplii were observed, one in mid-May and the other in the latter half of June. On both occasions approximately 3,000 per cubic meter were present. In contrast with *B. balanoides*, *B. crenatus* larvae showed only slight variation in size and setation from the description of the developmental stages given by Herz. During the period when *B. crenatus* larvae were present the temperature rose from 10° to 24° C., a greater range than that experienced by Herz's specimens.

From late July until early September, when the data stopped, nauplii of another species of *Balanus* were found. A few were also observed in November 1945. Presumably these were the nauplii of *Balanus eburneus*, since this is the time of year when this species breeds. These were never numerous; the highest number of 200 per cubic meter occurred in late July.

Aside from these forms, small cyprids appeared sporadically throughout the year. The majority of these were found from November to March, but occasional specimens were seen in April, June, and July. No nauplii appeared that could belong to the same species as these cyprids. The cyprids measured 0.4 mm. long by 0.25 mm. wide; of the barnacle larvae whose dimensions are known, only *Chthamalus stellatus* has a cyprid as small as this. It is probable that these are cyprids of *Chthamalus*, since *C. fragilis* and possibly *C. stellatus* occur in the Woods Hole region.

Gastropod Veligers

Table I shows that gastropod veligers were most abundant from May through July, with maximum numbers in June. No attempt has been made to identify them. According to Fish (1925), the bulk of planktonic gastropod larvae undoubtedly belong to the group of gastropods which discharge their eggs directly into the sea water. He found the eggs and larvae of *Littorina litorea* numerous from March to July, while those of *Lacuna vincta* were abundant in February also. Gastropod eggs were scarce in Tisbury Great Pond, only a few being observed in early March. Few gastropod veligers were present in April, but in May the numbers began to rise; the highest number of about 37,000 per cubic meter occurred in the latter part of June. A much smaller maximum appeared in late July. Gastropod veligers declined in abundance during the fall months of 1945, and none were found from December through February.

Lamellibranch Veligers

Table IV shows the period of occurrence in 1946 of the lamellibranch veligers which could be identified by means of Stafford's (1912) de-

TABLE IV. Period of Occurrance of Lamellibranch Veligers in 1946

	April	*May*	*June*	*July*	*August*
Mya arenaria	x	x	x	x	x
Mytilus edulis	x	x	x	—	—
Venus mercenaria	—	—	x	x	x
Ostrea virginica	—	—	x	x	x

scriptions and plates. *Mytilus edulis* veligers appeared infrequently and in small numbers, and therefore the period when they were observed is shorter than has been reported. Fish (1925) found these veligers in Woods Hole harbor from early June until late in the fall. The veligers of *Mya arenaria* were the dominant type in Tisbury Great Pond from late April into June and continued to appear throughout the summer. The veligers of *Venus mercenaria* were most abundant in late July and early August. None of these veligers could be identified in making the counts, and so quantitative estimates of their seasonal abundance cannot be given. However, at the end of July, *Venus* was by far the dominant form among the more than 10,000 veligers per cubic meter that were found at this time. Unfortunately the veligers in the 1945 fall samples were not sufficiently well preserved to allow their identification, but it is probable that *Venus* and *Mya* veligers were present. Only early veligers appeared during this period; possibly they were dead when caught by the net and this, too, may explain the distortion of the specimens.

Due to the greater development of the left umbo, it was possible to identify all but the earliest veligers of *Ostrea virginica* when making the counts. The asymmetry of the umbones was evident in specimens only 0.1 mm. in length. In 1945, the first oyster veliger was detected on June 24, but two weeks elapsed before significant numbers of these veligers appeared. During this summer only one maximum occurred on July 12, when nearly 15,000 per cubic meter were present. *Ostrea* veligers continued to be present in small numbers until mid-August. Since samples were taken every three days or so during the summer of 1945 it is unlikely that a maximum was missed, but it is surprising that only this one good-sized brood of veligers occurred.

In 1946, a few veligers, probably young stages of *Ostrea*, were found

on June 23. Later stages were present throughout July and August, but fewer were counted than in 1945. A small peak of veligers appeared in early July and a larger one of about 9,000 per cubic meter occurred at the end of July. Since no samples were taken between July 7–21, more veligers may have been present during this period.

The numbers of oyster veligers noted during both summers are small, but spawning may have been much more extensive than the figures given would indicate. Loosanoff (1932), who studied the distribution of oyster larvae in relation to currents and depth, found that the veligers remain on the bottom during most of their existence, swimming only when the current velocity is least. Probably the number of oyster veligers taken by the plankton sampler is only a small proportion of the numbers present between the surface and the bottom of the pond.

Judging from the times of appearance of the veligers, spawning did not occur in any intensity until the temperature of the water had reached 24° C. It is known that spawning may occur over a wide range of temperature, from 16.6° to 28° C. in Long Island Sound (Loosanoff and Engle, 1940). According to Medcof (1939), a rise in temperature when the oysters are ripe is more important than the actual temperature. Since the temperatures rose fairly steeply throughout June of both years and since the ages of the observed veligers are not known it is impossible to state with exactitude the times when spawning began.

Polychaete Larvae

Polychaete larvae occurred sporadically throughout the year, attaining maximum numbers in April and May (see Table I). Fig. 9 gives the quantitative data for 1946 in graphical form, plotted on a logarithmic scale. This shows the two major maxima which were found in April and May. Only *Synchaeta* and *Acartia* appeared in greater numbers during the year. In 1945, small maxima of polychaete larvae were observed every month from June to December, the largest number of about 1,700 per cubic meter occurring at the end of November.

A number of different species were present, but it has been impossible to identify them properly. The dominant forms were spionid larvae. The April maximum consisted almost entirely of so-called spionid "metatrochophores." Species of *Polydora* were undoubtedly present,

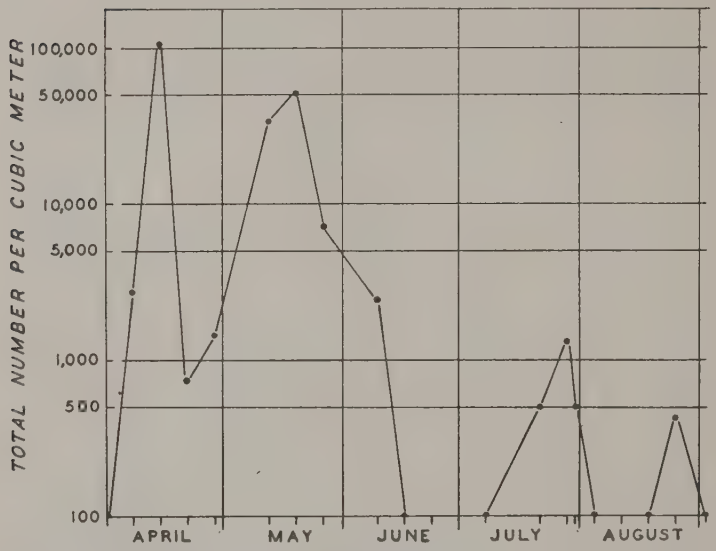

Figure 9. The total number per cubic meter, on a logarithmic scale, of polychaete larvae from April through August 1946.

since some later stages of spionid larvae appeared identical in morphology and pigmentation to Thorson's (1946, fig. 42) figure of *Polydora ciliata* Johnst. Another larva, which occurred in limited numbers in April and May, is probably *Nereis pelagica* Linn., as it is similar to Thorson's (1946, fig. 29) and to D. P. Wilson's (1932) figures of this species. Other larval forms probably include species of *Nephthys* and possibly of *Mystides.*

The Rotifer Population

Synchaeta littoralis: present throughout year.
Temperature range: 0°–25° C.
Extreme salinities: less than 1–31°/₀₀
Synchaeta sp.: late October 1945 to February 1946
Temperature range: 0°–13° C.
Extreme salinities: less than 1–20.3°/₀₀

The rotifer population consisted of two species of which *Synchaeta*

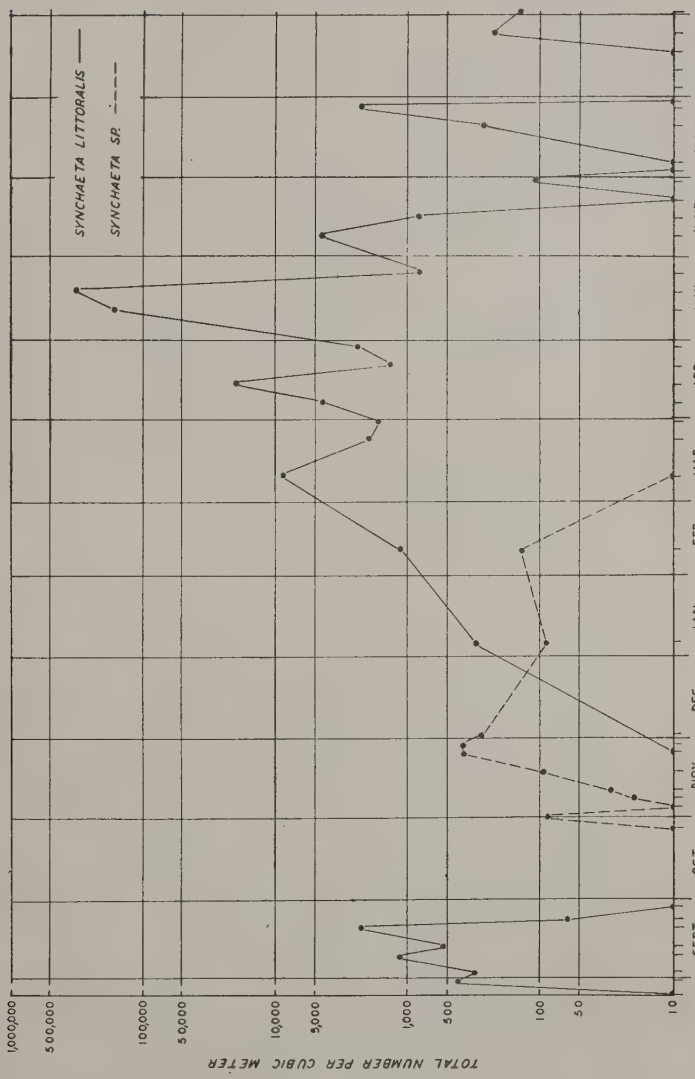

Figure 10. The total numbers per cubic meter, on a logarithmic scale, of *Synchaeta littoralis* and *Synchaeta* sp. from September 1945 through August 1946.

littoralis Rousselet was by far the dominant form. According to Rousselet (1902), who described *S. littoralis* from brackish water on the English and Scottish coasts, this species prefers the warmer spring months but is erratic in its appearance. This was found to be the case in Tisbury Great Pond.

The total numbers per cubic meter of the two species of *Synchaeta*, plotted on a logarithmic scale, are given in graphical form in Fig. 10. This shows that the greatest numbers of *S. littoralis* appeared from March to May. In mid-May this species attained a higher maximum than any other member of the zooplankton at any time during the year, when 315,000 per cubic meter were present. During the period when this greatest rise in numbers occurred the temperature rose from about 11° to 14.7° C. The salinity was relatively high at this time, ranging between 25 and 29‰. However, the appearance of *S. littoralis* at all times of year provides proof that it is both widely euryhaline and eurythermal. *Synchaeta* sp., on the other hand, preferred the late fall to winter months and was never abundant.

Podon polyphemoides (Leuckart)

Fairly abundant May–June
Temperature range: 11°–24° C.
Extreme salinities: 13.7–29.2‰.

Podon polyphemoides appeared in numbers in Tisbury Great Pond only during May and June. Several specimens were observed in March, but no more were seen until late April. Fig. 11, which gives the total number per cubic meter in graphical form, shows clearly the abrupt rise and fall in numbers of the *Podon* population. The highest maximum was reached in the third week of June. This was followed by such a sudden decrease in numbers that by the end of the month *Podon* had virtually disappeared. The picture was the same in 1945, although the estimated numbers were not as great; since a No. 2 net was used for the May sample the smaller individuals were not retained. As in 1946, by July 1 few *Podon* remained and the sample contained dead specimens.

Podon polyphemoides is predominantly a neritic cladoceran, extraordinarily euryhaline and moderately eurythermal. It is a cold water form and, according to Baker (1938), it is virtually absent from about Lat. 40° N. to Lat. 20° S. On the Northeast Atlantic coast of the

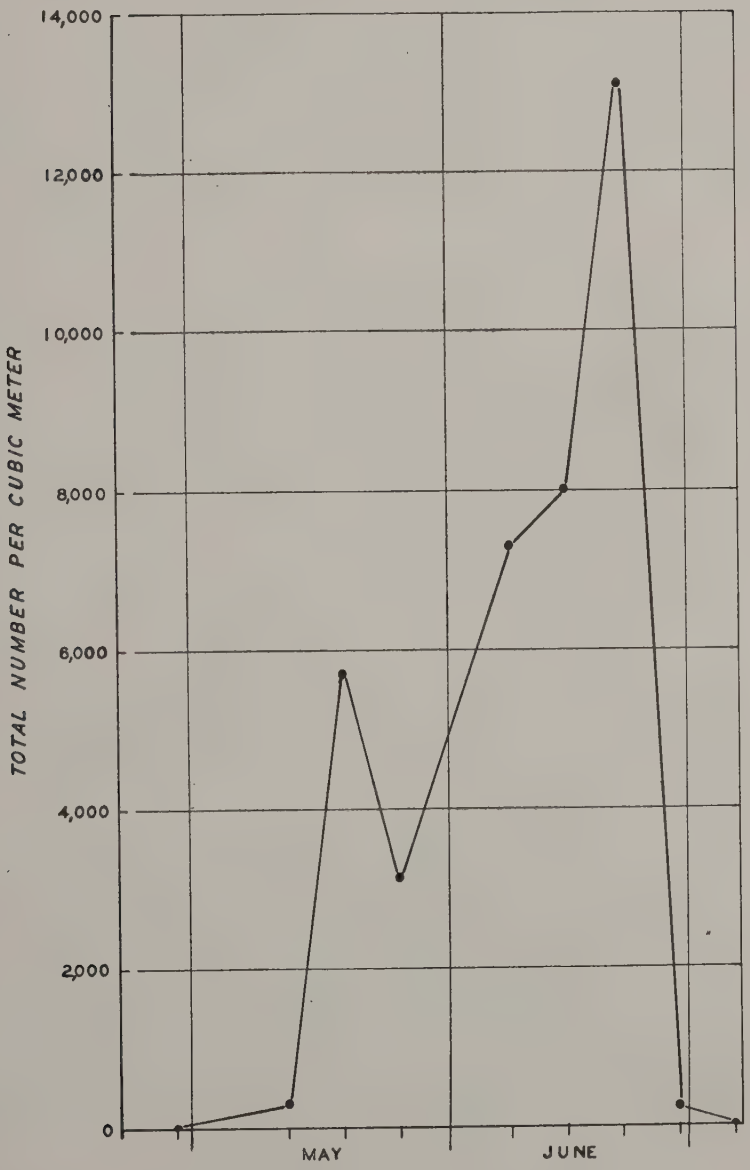

Figure 11. The total number per cubic meter of *Podon polyphemoides* for May and June 1946.

United States *P. polyphemoides* has been definitely recorded as far south as New Haven Harbor in Long Island Sound (Fish, 1925), although Bigelow and Sears (1939) reported *Podon*, species not given, as present between the offings of Marthas Vineyard and Chesapeake Bay.

Baker stated that *P. polyphemoides* has been known to withstand sudden extreme changes in salinity, from 1.05 to 35.1‰. Therefore the variations in the salinity of Tisbury Great Pond were well within its range.

However, the thermal preferences of *Podon* explain, at least in part, the period of its occurrence in the pond. Baker gave its optimal thermal range as 10° to 15° or 16° C., although it has been recorded at temperatures as low as 2.46° C. and as high as 19.8° C. During May the temperature rises rapidly in Tisbury Great Pond from about 11° C. to over 20° C., so that the period of optimum temperatures is short indeed. During the latter part of June when *Podon* was most abundant, the temperature was 21.7° C. This is probably the highest temperature at which *P. polyphemoides* has been recorded in numbers. *Podon* appeared when the temperature was about 11° C. and disappeared both summers at the beginning of July when the temperature exceeded 24° C. It seems obvious that temperatures in the vicinity of 24° C. are lethal to the population of *Podon polyphemoides*.

Forms Entering the Pond Accidentally

Chaetognaths are the most important organisms in this category in that they were fairly numerous for a short period, but several littoral copepods also appeared in small numbers after the opening of the beach. Table V lists the species and shows the months when they occurred.

Temora longicornis (Müller) and *Tortanus discaudatus* (Thompson and Scott) were found consistently in the samples during the period of their occurrence, while the other two calanoids appeared much more infrequently. These species were present only while the salinity was relatively high, between 25 and 31‰. Although Bigelow (1926) recorded a wide temperature and salinity tolerance for *Temora longicornis*, this species has not proved itself to be more than moderately euryhaline and eurythermal in Tisbury Great Pond. *Oithona similis* Claus entered the pond nearly every time the beach was opened during the period studied but never became established there. *Eurytemora herdmani* Thompson and Scott, not listed in Table V, was found on

only one occasion immediately after the opening of the beach in May 1945.

TABLE V. Times of Occurrence of Adventitious Forms

	1945		1946				
	June	*Sept.*	*Mar.*	*Apr.*	*May*	*June*	*July*
Temora longicornis	—	—	—	x	x	—	x
Tortanus discaudatus	—	—	x	x	x	—	—
Pseudocalanus minutus	—	—	—	x	x	—	—
Pseudodiaptomus coronatus	—	x	x	—	—	—	—
Oithona similis	x	x	x	x	x	—	x
Sagitta sp.	—	—	x	x	—	—	—

The Chaetognaths were most abundant in mid-April when 2,300 per cubic meter were present. These belong to the genus *Sagitta*, but the species has not been determined, since all the specimens were immature. They may be *S. elegans*, since Clarke and Zinn (1937) and Bigelow and Sears (1939) reported swarms of this species off Marthas Vineyard in April or May. The sagittae did not remain in the pond but disappeared rapidly.

THE PHYTOPLANKTON

The phytoplankton counts include the period from September 13, 1945 to September 2, 1946. Fig. 12 gives the total phytoplankton as cells per liter as well as the total zooplankton in numbers per cubic meter. Table VI shows, semiquantitatively, the seasonal abundance of the diatoms, dinoflagellates, and flagellates that occurred in greatest numbers. From this it is apparent that diatoms were present throughout the year, while flagellates and dinoflagellates were most abundant during the summer months. The highest maximum of diatoms occurred in January when a count of 350,000 cells per liter was obtained. Large numbers were also present in February, during the latter half of May, and from September to December. The dinoflagellates were most abundant in late April, late June, and late July. In mid-August *Euglena* occurred in greater numbers than any other organism during the year, when 855,000 cells per liter were present.

In general, the cycle of the phytoplankton of Tisbury Great Pond differs from that of oceanic areas in that diatoms are fairly abundant throughout the year, with only one pronounced maximum in January.

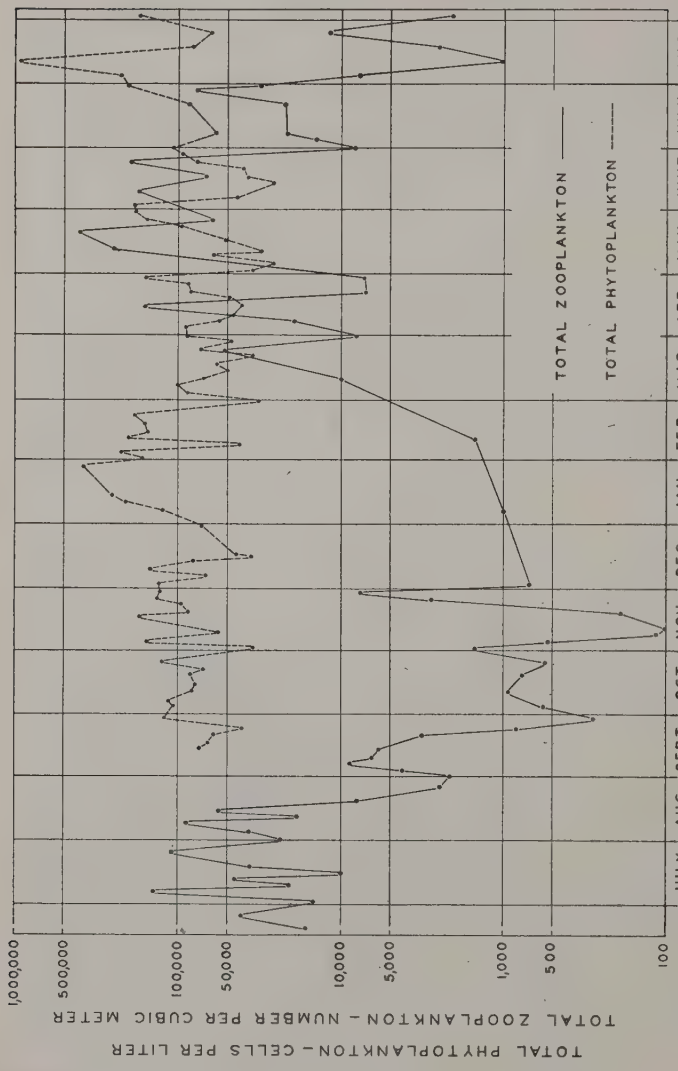

Figure 12. The total numbers of phytoplankton as cells per liter from September 1945 to September 1946 and the total numbers of zooplankton per cubic meter from June 1945 to September 1946.

TABLE VI. Seasonal Cycle of Abundance of the Major Elements of the Phytoplankton
x: 1,000–10,000; xx: 10,001–100,000; xxx: 100,001–1,000,000. Semiquantitative, as Cells per Liter.

	1945				1946							
	Sept.	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
DIATOMS:												
Skeletonema	xx	xx	xx	xx	xxx	xx	xx	x	x	—	—	x
Navicula	x	x	x	x	x	x	xx	x	x	x	x	x
Nitschia	x	x	x	—	—	xx	x	x	x	—	x	x
Melosira	xx	xx	xx	xx	xx	x	xx	xx	x	x	x	—
Lichmophora	x	xx	x	—	—	—	—	—	—	—	x	x
Chaetoceros	—	—	—	—	—	xx	x	x	xx	xx	xx	x
Pleurosigma	—	x	—	—	—	—	x	x	x	—	—	—
DINOFLAGELLATES:												
Peridinium	—	—	—	x	x	x	—	—	x	x	—	xx
Prorocentrum micans	—	—	—	—	—	—	—	—	—	xx	xx	xx
Dinophysis	—	—	—	—	—	—	—	—	—	x	—	—
Gymnodinium	—	—	—	—	—	—	—	xx	—	x	xx	xx
FLAGELLATES:												
Eutreptia	x	x	xx	x	—	—	—	—	—	—	x	xx
Euglena	—	—	—	—	—	—	—	—	—	—	x	xxx

DISCUSSION AND CONCLUSIONS

The Composition of the Zooplankton Population

Most of the zooplankton organisms of Tisbury Great Pond live a precarious existence. To survive successfully throughout the year under present conditions, each species must be able to tolerate and to thrive on extremes of salinity and temperature. Except for accidental visitors, the organisms living in the pond are both euryhaline and eurythermal, at least to a considerable extent. Environmental conditions are far more rigorous than those of any oceanic area. For this reason it is of interest to know what species are capable of living in Tisbury Great Pond as well as the degree to which they are acclimated to its conditions.

In general, several categories of organisms occur:

1. Extremely euryhaline and eurythermal species, present at all seasons. None of the calanoid copepods belong in this group, and it is questionable whether any harpacticoids do, since they rarely occurred in numbers in the plankton samples. *Halicyclops magniceps* appeared erratically throughout the year and probably belongs in this category, as does *Synchaeta littoralis*. Both of these have long been known as brackish water species.

2. Fairly euryhaline and eurythermal species surviving unfavorable conditions either as resting stages or in small numbers. As stated, this category includes forms for which either the salinity or the temperature range is too great or the change of either too abrupt. The majority of the zooplankton living in the pond with any degree of permanence should fall in this general group, but it is extremely difficult to draw hard and fast lines for them. Because of the special conditions in Tisbury Great Pond, due to the periodic opening of the beach, any organism surviving in the pond for any length of time must be fairly euryhaline; this implies a wide salinity range a bit short of complete euryhalinity.

The organisms most affected by temperature are *Acartia clausii*, *A. tonsa*, *Eurytemora hirundoides*, and *Centropages hamatus*. *Acartia clausii* disappeared from the samples when the temperature rose to about 24° C., while *A. tonsa* was not found until the temperature was about 20° C. and was abundant only during the period when the temperature varied between 20° and 25° C. This implies that *A. tonsa* has an exceptionally narrow temperature range, but the fact that it has

been taken in numbers in January in Long Island Sound proves that a factor other than temperature is responsible for its limited period of abundance in the pond. Both *Eurytemora hirundoides* and *Centropages hamatus* are winter-to-late-spring forms with a temperature range similar to that of *Acartia clausii*. Both of these species may be considered members of the pond fauna, and not adventitious species, although *Centropages hamatus* in particular was never abundant. It is perhaps possible that the competition of the other organisms occurring during the spring months was too great for either *E. hirundoides* or *C. hamatus* to become fully established.

Despite the fact that *Acartia tonsa* has a wide salinity range, a steep rise in salinity during both summers coincided with an abrupt decrease in numbers of the population. Since this occurred during its period of optimum temperatures, it seems to indicate that *A. tonsa* is not sufficiently heteroeuryhaline to withstand readily a sudden rise in salinity, although it is tolerant to great variations in salinity when the change occurs gradually. The problem of the true limits of tolerance of *A. tonsa* to varying temperatures and salinities cannot be resolved with the available data.

3. Extremely euryhaline and moderately eurythermal species. *Podon polyphemoides* is the only member of this category. Its thermal range is more limited than that of the other organisms mentioned, since it appeared at about 12° C. and disappeared as the temperature rose to 24° C.

4. Larval forms, presumably of adult species that live in the pond and are adapted to its conditions. The three species of *Balanus* nauplii found, for example, are the young of barnacles suited to this environment. Since these organisms occur in the plankton only during their larval stages, they cannot be considered permanent members of the zooplankton and therefore require a separate category.

5. Adventitious species. This could include both neritic and oceanic forms, but only predominantly neritic species were brought into the pond when the beach was opened. The sagittae belong in this category. Undoubtedly the littoral copepods *Tortanus discaudatus*, *Temora longicornis*, *Pseudocalanus minutus*, and *Oithona similis* may be included here, since none of these species became established in the pond. It is probable that *Paracalanus crassirostris* is a member of this group.

Oithona brevicornis is an adventitious species that has proved itself capable of surviving and reproducing in this environment. That this is so is shown by its continuous presence in the pond during the last half year of the observations, and also by the appearance of maximum numbers of adults after the pond was closed.

In conclusion, almost no members of the zooplankton community are capable of living in the surface layers of Tisbury Great Pond throughout the year. The rotifers are the only forms that appear at all seasons. Temperature is the more important factor limiting the periods of occurrence of the majority of organisms living in the pond, since they must, of necessity, be fairly euryhaline in order to survive there. On the other hand, the range of salinity is a significant factor, in that it bars from the pond the littoral forms that would appear in greater abundance if the outlet were always open, as in estuarine situations. In contrast with oceanic areas, the pond is poor in numbers of species of calanoid copepods, because few calanoids are capable of tolerating such a range of salinity.

The Seasonal Cycle of the Total Zooplankton

The cycle of the total zooplankton in numbers per cubic meter is shown in Fig. 12, which also portrays the total phytoplankton as cells per liter. The seasonal change in numbers of the zooplankton was pronounced. During the period from late August to January, copepods virtually disappeared from the samples and almost no zooplankton was present, except for occasional bursts of *Synchaeta*, polychaete larvae and veligers. In early January a few copepods appeared, rotifers were increasing in numbers, and a few barnacle larvae were present. The quantity rose barely perceptibly to March, when *Synchaeta* and *Eurytemora* produced a maximum. The mid-April maximum was due largely to polychaete larvae with rotifers second in numbers and copepods a poor third. The May peak was predominantly *Synchaeta*, with polychaete larvae and *Acarta clausii* contributing in appreciable numbers. During June, *A. clausii* occurred in greatest abundance, with gastropod veligers numerically second. *A. clausii* disappeared in early July as *A. tonsa* appeared abruptly with its maximum at this time. The data for the two summers show clearly how the sudden decrease in the *A. tonsa* population left low numbers of zooplankton in the pond.

Essentially, therefore, there was but a single maximum in the zoo-

plankton, although this covered the period from March to July or August. This cycle of the zooplankton is obviously not correlated directly with temperature, even though temperature must be one of the most important factors. The numbers began to increase gradually in January when temperatures were minimal and the pond frozen. A barely perceptible rise in numbers continued to March, but during this and the succeeding months to July or August, when the temperature had reached its highest point, maximum followed maximum. From this time to December there was an impoverishment of the zooplankton. The temperature was high at least until mid-September, but no autumn maximum occurred. Since the numbers were low while the temperature was falling and high while it was rising, the correlation coefficient between total zooplankton and temperature is close to zero. On the other hand, the correlation coefficient between total copepods and temperature is barely significant, 0.282, because the two species of *Acartia* attained their maximum numbers when the temperature was above 20° C.

The lack of a linear correlation between zooplankton and temperature may be explained by the fact that the real relationship between numerical abundance of organisms and temperature is complex. When the total numbers of copepods per cubic meter are plotted against temperature, as in Fig. 13, the result is a wide scattering of points. However, a dot diagram prepared for a single species, such as that shown in Fig. 14 for *Acartia clausii*, takes the form of a curve with a rising and a falling limb. This means that the numbers increase as the temperature rises to an optimum and then decrease as the temperature continues to mount. If the total zooplankton consists of organisms with similar temperature curves, obviously no straight-line correlation between zooplankton and temperature can exist.

That an abundance of food was available to the zooplankton throughout the year is evidenced by the phytoplankton counts shown in Fig. 12. Diatoms were abundant for the greater part of the year, while flagellates and dinoflagellates were maximal during the summer months. The phytoplankton shows but two pronounced peaks, the January diatom maximum and the August maximum largely made up of *Euglena*. There was no pronounced autumn diatom maximum, but diatoms were plentiful during the fall months. In this case, also, there is no direct correlation between the total zooplankton and the total phytoplankton, the coefficient obtained being negative but insignifi-

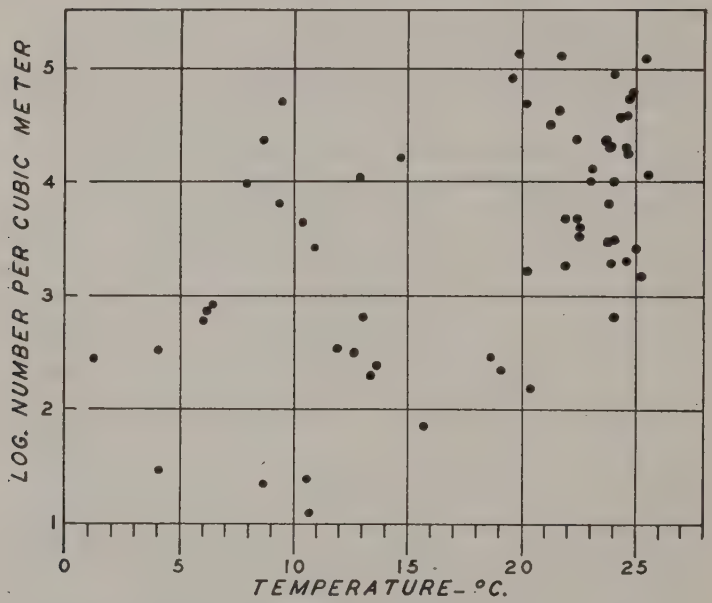

Figure 13. The relation between the total number of copepods of all stages, plotted on a logarithmic scale, and temperature.

cant. It is true that the zooplankton began to increase to a maximum after the January diatom maximum, but it decreased after the August peak. Phytoplankton was always abundant, while the zooplankton was never so plentiful as to give evidence of any appreciable "grazing" of the phytoplankton.

Neither zooplankton nor phytoplankton shows any correlation with salinity. This is not surprising, since all the organisms occurring in any numbers in the pond are fairly euryhaline. The variability of the salinity may act as a complicating factor, reducing the intelligibility of the other relationships. It has already been noted that at least one dominant species, *Acartia tonsa*, may not be sufficiently heteroeuryhaline to withstand successfully the rapid increase in salinity attendant upon the opening of the beach. In this case, also, there is no simple correlation, since, although the numbers decrease with rising salinity,

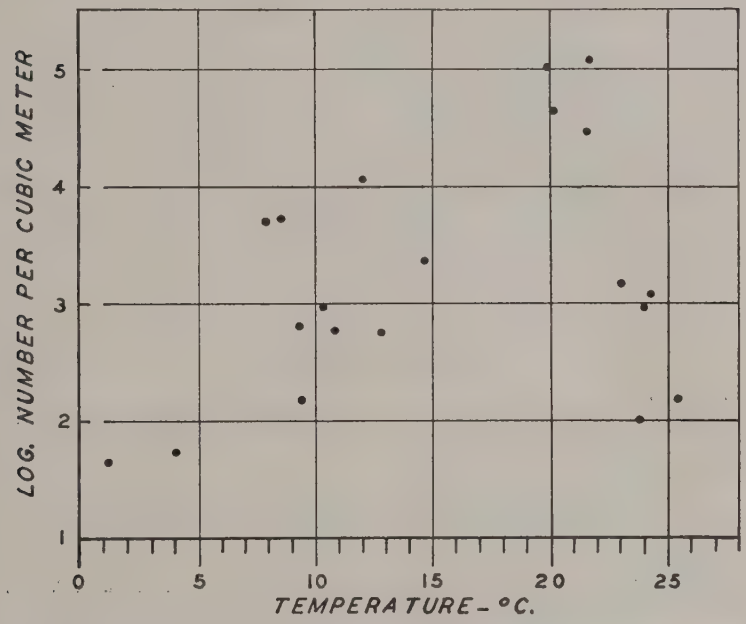

Figure 14. The relation between the total number of copepodids and adults of *Acartia clausii*, plotted on a logarithmic scale, and temperature.

they fail to increase as the salinity falls. Perhaps the opening of the beach in August of both summers may be in part concerned in the paucity in numbers of zooplankton during the fall months.

From the foregoing paragraphs it is evident that the zooplankton had a pronounced seasonal cycle with a single late spring maximum, and that its abundance was not directly related to the temperature or the salinity or the phytoplankton. The effect of temperature on the zooplankton population was marked, for the zooplankton increased in numbers as the temperature rose, but when maximum temperatures were reached the zooplankton decreased in abundance. That the real relationship between the temperature and the total quantity of organisms is complex is shown by the temperature curves of individual species. Any effects of the varying salinity, however, were not clearly reflected in the abundance of the total zooplankton, since the latter increased or decreased regardless of salinity conditions. There is one

exception to this, for it has been shown that the rising salinities, through their possible effect on the dominant summer species, may have been involved in the diminution in numbers of the total zooplankton that occurred in August. The phytoplankton, on the other hand, showed no relationship with the zooplankton, since it was always abundant regardless of whether the zooplankton was increasing or decreasing in numbers. Presumably because the zooplankton consisted of organisms with widely varying requirements in these respects, the total number of zooplankton showed no direct relationships with temperature, salinity, or total phytoplankton.

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Contribution No. 392

Reprinted from Ecology, Vol. 29, No. 1, January, 1948
Printed in U. S. A.

OBSERVATIONS ON THE ABNORMAL DEVELOPMENT AND GROWTH OF BARNACLES AS RELATED TO SURFACE TOXICITY[1]

The deformation of barnacle shells has been observed to result from several factors. Moore ('35) noted this behavior as a result of crowding, while Bärenfänger ('38) reported on the action of barnacles in digging into soft paint surfaces, which produced arched bases. Pomerat and Weiss ('46) observed that the growth of some species of barnacles on certain substrates resulted in specimens with deeply scalloped margins instead of the typical smooth edge, suggestive of localized marginal growth

[1] Contribution No. 392 from the Woods Hole Oceanographic Institution.

interruptions. In addition, on several soft substrates such as paraffin, barnacles were found with distinctly concave bases. The observations reported in this note extend the information on the abnormal development of the base and shell of barnacles with relation to paint and metal surfaces of different degrees of toxicity.

Results

In many examinations of antifouling paints exposed to marine fouling, barnacles were found so loosely attached to paint surfaces that a very slight pressure was sufficient to remove them. In addition, the peripheral edge of the shell was usually deeply scalloped and the plates of the shell distorted. The bases of these barnacles were also characterized by an increased opaqueness of the radial canals, which is probably indicative of heavier depositions of calcium carbonate than found in the normal specimens. Without exception, barnacles exhibiting these malformations were loosely attached to the toxic surface and were easily removed. This condition was restricted to specimens attached to paints pigmented principally with copper. Examples of these abnormalities are illustrated in figure 1. It is of interest to note that the three common barnacles found in Biscayne Bay, Florida, *Balanus amphitrite, Balanus improvisus,* and *Balanus eburneus,* exhibited in order decreasing resistance to the development of malformations. This is the same order of decreasing tolerance to copper that was found for these three species in another investigation (Weiss, '47).

Barnacles which had attached to copper al-

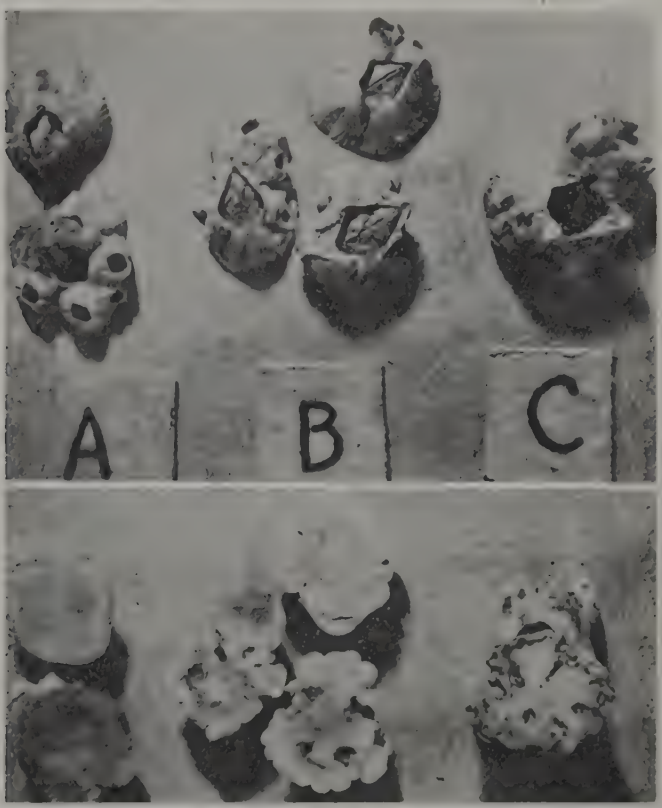

Fig. 1. Examples of deformed barnacles as found on a copper paint surface. The top and bottom views are of the same barnacles. The vertical rows, designated A, B, and C, represent specimens of *B. amphitrite, B. improvisus,* and *B. eburneus,* respectively.

loys showed similar malformations. Four specimens of *B. amphitrite* which had attached to an alloy containing 45 per cent nickel and 55 per cent copper exhibited four degrees of development of the thickened and malformed base. In figure 2, photomicrographs of their bases are shown.

Specimens of *B. improvisus* and *B. eburneus* which had attached close to but not directly on a copper surface, paint or metal, were also found to be malformed. It is apparent that the copper dissolving and diffusing from the toxic surface is capable of affecting the barnacle and producing a reaction similar to that found in specimens attached directly to the paint or metal surface.

The abnormality of the base and shell was also noted on specimens removed from zinc and galvanized surfaces but not from lead surfaces. Examples of specimens from zinc and lead are shown in figure 3. The adhesion of the barnacles to the zinc surfaces was very poor, while those attached to lead were difficult to remove.

Barnacles that attached to paints pigmented with mercury always adhered to the surface

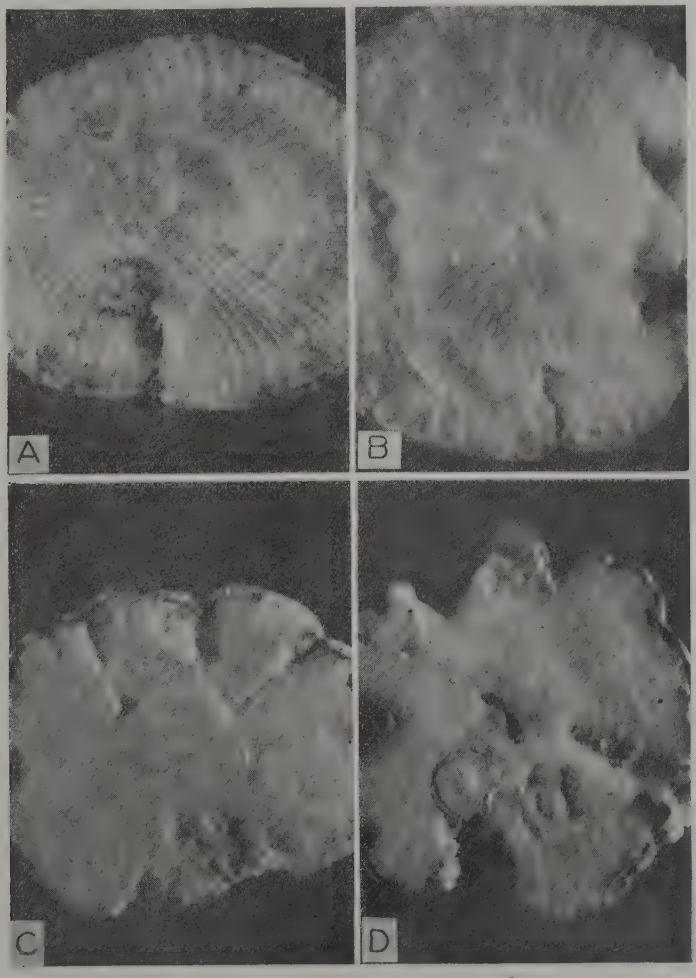

FIG. 2. Photomicrographs of the bases of four specimens of *Balanus amphitrite* as found on a nickel-copper alloy. Note the correlation of increase in margin deformation with increase in basal thickening.

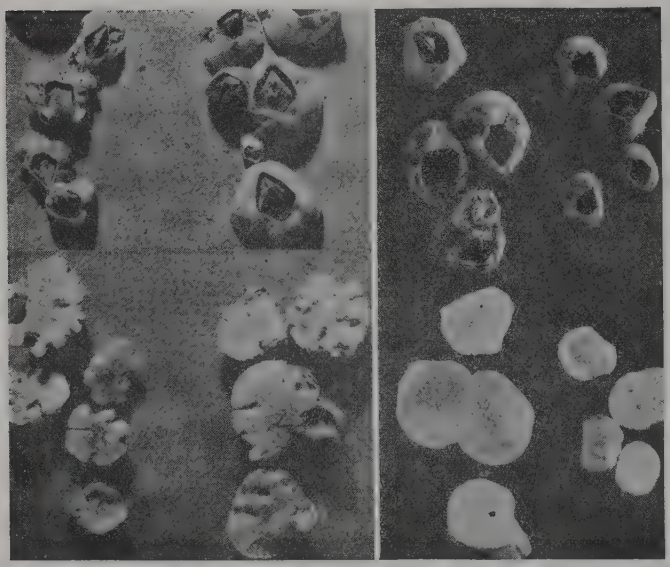

FIG. 3. Specimens of barnacles removed from zinc and zinc coated surfaces, left photograph. The scalloped margins and basal thickening resemble that found on specimens removed from copper surfaces. Right photograph, specimens of barnacles removed from lead surfaces. No shell deformation is evident except edge flattening due to crowding. The apparent basal thickening is due to the adhesion of lead corrosion products to the bases.

and showed no abnormality of their basal plates. No specimens could be satisfactorily removed for basal examination, their adhesion being too firm. The abnormal basal formations reported above with concomitant poor adhesion of the barnacles may serve to indicate lines of investigation for further study of barnacle adhesion.

SUMMARY

Barnacles attached to and growing on copper antifouling paints, copper alloys, and zinc were found to have the edge of the base deeply scalloped and the plates of the shell distorted. These specimens also had an excessive calcification of the base and were loosely attached to the substratum. This reaction was not found in barnacles attached to mercury antifouling paints or lead surfaces.

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Contribution No. 393

Reprinted from JOURNAL OF THE FRANKLIN INSTITUTE,
Vol. 245, No. 5, May, 1948
Printed in U. S. A.

DIMENSIONAL ANALYSIS: AN APPROACH FROM TRANSFORMATION THEORY AND A CRITERION FOR SCALING MODEL EXPERIMENTS.[1]

BY

J. C. DECIUS.[2]

1. THE INVARIANTS OF CONTINUOUS TRANSFORMATION GROUPS.

In a recent article in this journal, Langhaar (1)[3] has drawn attention to a method of dimensional analysis in which the kinds of physical quantities are explicitly given a vector representation. The crucial theorem of this subject was proved by Langhaar in terms of theorems on homogeneous functions.

The author of the present paper has formalized the subject matter of dimensional analysis from a slightly different mathematical point of view, in which, however, as is natural, the material receives a practically identical representation. Because of the relationship of the following method to a very general method of discussing problems in mathematical physics, it seems worth-while to set it forth here. In addition, since the development is aimed at the treatment of scaling laws for model experiments, a new criterion is given for the possibility of satisfying the scaling laws when certain restrictions are imposed upon the variables.

A fruitful approach to the problems of dimensional analysis may be made by regarding any physical equation as the expression of an invariant under the transformations of some group. Frequently the knowledge of some form of spatial symmetry, the requirement of invariance under permutation of indistinguishable particles, or the necessity of special invariant properties which must obtain under transformations simultaneously involving temporal and spatial coordinates has been used to simplify or actually to advance the mathematical description of the physical world. Although the results of the following application of invariant theory are all rather well known, the method itself is rather elucidating, particularly with regard to the derivation of the laws of similitude which govern the scaling of model experiments.

It will be shown below that all of the results of dimensional analysis follow from the single postulate that all physical relations must be expressible in a form which does not depend upon the "magnitude" of the various physical units of measurement requisite for the description of a given physical situation.

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[1] Contribution No. 393 from the Woods Hole Oceanographic Institution.

[2] Woods Hole Oceanographic Institution, Woods Hole, Mass.; now at Brown University, Providence, Rhode Island.

[3] The boldface numbers in parentheses refer to the list of references appended to this paper.

Such changes of unit magnitude form the representation of a group of continuous transformations. A group of continuous transformations may be represented by the equations:

$$\bar{x}^i = \xi^i(x^1, x^2, \cdots x^n; \quad \lambda^1, \lambda^2, \cdots \lambda^m), \qquad i = 1, 2, \cdots n \tag{1.1}$$

in which the barred quantities are the new values of the variables, which were originally $x^1, x^2, \cdots x^n$, after the transformation induced by the set of continuously variable, independent parameters, $\lambda^j (j = 1, 2, \cdots m)$. The usual postulates for a group require that the λ^j can assume such values as will:

1. Induce the identity transformation

$$x^i = \xi^i(x^1 \cdots x^n; \quad \lambda_0{}^1 \cdots \lambda_0{}^m).$$

2. Induce the resultant of two or more successive transformations in one step, that is, if

$$\bar{x}^i = \xi^i(x^1 \cdots x^n; \quad \lambda_1{}^1 \cdots \lambda_1{}^m),$$
$$\bar{\bar{x}}^i = \xi^i(\bar{x}^1 \cdots \bar{x}^n; \quad \lambda_2{}^1 \cdots \lambda_2{}^m),$$

then

$$\bar{\bar{x}}^i = \xi^i(x^i \cdots x^n; \quad \lambda_{12}{}^1 \cdots \lambda_{12}{}^m).$$

3. Induce a transformation "inverse" to every given transformation, that is, if

$$\bar{x}^i = \xi^i(x^1 \cdots x^n; \quad \lambda_1{}^1 \cdots \lambda_1{}^m),$$
$$x^i = \xi^i(\bar{x}^1 \cdots \bar{x}^n; \quad \lambda_{-1}{}^1 \cdots \lambda_{-1}{}^m).$$

It may then be shown that the equations of transformation (1.1) determine a set of linear partial differential operators

$$U_j = \left(\frac{\partial \xi^i}{\partial \lambda^j}\right)_0 \frac{\partial}{\partial x^i} \tag{1.2}$$[4]

which represent the independent infinitesimal transformations of the group (the subscript zero for $\partial \xi^i / \partial \lambda^j$ implies that the derivative is to be evaluated for those values of the parameters, λ^j, which induce the identity transformation; without loss of generality these values may henceforth be assumed to be zero). The most general infinitesimal transformation is represented by

$$U = \alpha^j U_j \tag{1.3}$$

in which the α^j are arbitrary constants; any finite transformation is

[4] The summation convention of tensor notation is used throughout. Thus $\left(\frac{\partial \xi^i}{\partial \lambda^j}\right)_0 \frac{\partial}{\partial x^i}$ implies $\sum_{i=1}^{n} \left(\frac{\partial \xi^i}{\partial \lambda^j}\right)_0 \frac{\partial}{\partial x^i}$; this is true only if the index appears in one place as a superscript, in another place as a subscript.

generated by an integration of the differential operation signified by (1.3).

The important consequence for the present purposes is that if any function of the variables x^i, say

$$F(x^1, \cdots x^n) = 0, \tag{1.4}$$

is known to be invariant under the group represented by (1.1), then it is always possible to express (1.4) in terms of a complete set of fundamental invariants $y^1, y^2, \cdots y^{n-r}$, which are determined by

$$Uy = 0 \tag{1.5}$$

as functions of the x^i. Thus

$$F(x^1, \cdots x^n) = \Phi(y^1, \cdots y^{n-r}) = 0 \tag{1.6}$$

and the number of independent variables has been reduced by r, which is equal to the rank of the matrix $\left\| \left(\frac{\partial \xi^i}{\partial \lambda^j} \right)_0 \right\|$.

2. DETERMINATION OF THE INVARIANTS OF A GENERAL PHYSICAL EQUATION UNDER TRANSFORMATIONS OF THE UNITS.

The nature of the number, x^i, resulting from a physical measurement of the jth kind of physical quantity is such that it is determined only within a transformation of the type:

$$\bar{x}^j = \exp [\lambda^j] x^j, \qquad -\infty < \lambda^j < +\infty. \tag{2.1}$$[5]

If it is desired to deduce the possible kinds of functions of the *magnitudes* of a basic set of physical quantities, which give the *magnitude* of a resultant physical quantity derivable from the basic ones, it is possible to apply the principles of Section 1 in the following manner. The resultant magnitude itself must obey a transformation law of the same form as (2.1)

$$\bar{x} = \exp [f(\lambda^j)] x \tag{2.2}$$

in which the value of f may be taken as zero when $\lambda^j = 0$, all j. Then Eq. 1.3 requires that the relation between x and x^i be expressible in terms of a function y determined by

$$\alpha^k \left[\delta_k{}^i x^k \frac{\partial y}{\partial x^i} + \left(\frac{\partial f}{\partial \lambda^k} \right)_0 x \frac{\partial y}{\partial x} \right] = 0. \tag{2.3}$$

The α^k being arbitrary constants, (2.3) is equivalent to the m relations

$$\frac{\partial y}{\partial \ln x^k} = -\left(\frac{\partial f}{\partial \lambda^k} \right)_0 \frac{\partial y}{\partial \ln x}, \qquad k = 1, 2, \cdots m. \tag{2.4}$$

[5] It is clear that the range of the λ^j indicated will contain values satisfying all the group postulates of Section 1.

An acceptable solution of this system is

$$y = \prod_{k=1}^{m} \frac{(x^k)^{a_k}}{x}, \tag{2.5}$$

where $a_k = \left(\frac{\partial f}{\partial \lambda^k}\right)_0$ is a constant, so that, y being actually an invariant, which can be assumed to have the numerical value of unity, the acceptable form for the combination of magnitudes is

$$x = \prod_{k=1}^{m} (x^k)^{a_k} \tag{2.6}$$

with the transformation law:

$$\bar{x} = \exp\left[a_k \lambda^k\right] x. \tag{2.7}$$

It is immediately perceived that the numbers a_k characterize the *kind* of the derived quantity and that they may be regarded as the components of an m-dimensional vector in the basis in which the lth component of the kth fundamental quantity is the Kronecker symbol, $\delta_1{}^k$. In other words, the general symbol, $a_j{}^i$, is the ordinary exponent occurring in the conventional dimensional formula for the ith *kind* of variable relative to the jth fundamental *kind* of quantity; for example, let $i = 1$ designate energy; $j = 1, 2, 3$ correspond to mass, length, and time, respectively, then $a_1{}^1 = 1$, $a_2{}^1 = 2$, $a_3{}^1 = -2$.

Now let x^i be a set of derived magnitudes expressible in terms of the basic set, x^j. Then the transformation laws are:

$$\begin{gathered} \bar{x}^i = \exp\left[a_j{}^i \lambda^j\right] x^i, \\ i = 1, 2, \cdots n; \quad j = 1, 2, \cdots m. \end{gathered} \tag{2.8}$$

Now let

$$F(x^i) = 0$$

be the expression of an unknown physical relation in terms of the magnitudes, x^i. Equations 1.2, 1.3, and 1.5 require that the relation be expressible in terms of y^k, the solutions of

$$\alpha^i a_j{}^i x^i \frac{\partial y^k}{\partial x^i} = 0$$

or

$$a_j{}^i \frac{\partial y^k}{\partial \ln x^i} = 0 \tag{2.9}$$

$$\text{for} \quad j = 1, 2, \cdots m.$$

Solution of Eq. 2.9 gives

$$y^k = \prod_{i=1}^{n} (x^i)^{b_i^k}, \tag{2.10}$$

$$k = 1, 2, \cdots n - r,$$

where the b_i^k are constants determined by

$$a_j^i b_i^k = 0 \tag{2.11}$$

and where r is the rank of the matrix $\|a_j^i\|$.

This result is, of course, the well-known "π-theorem" as described by Buckingham (2) or Bridgman (3). The virtue of having used the transformation theory lies chiefly in the following two points:

1. The "alias-alibi" duality of any transformation immediately allows the conclusion that although the deductions were based on the assumption that the "absolute" magnitude of the physical quantities were unchanged during the transformation, the invariants, y^k, will certainly satisfy the equation

$$\Phi(y^k) = 0$$

throughout a transformation in which the fundamental magnitudes are fixed and the magnitudes of the x^i are "actually" changed but in such a way as to keep the y^k constant. In other words, empirical physical information satisfying

$$F(x^i) = 0$$

on a given *scale* may be used to predict a physical relation on any other scale, provided only that the x^i are varied in such a way as to maintain the constancy of the y^k.

2. The simplification of a physical problem brought about by the reduction of the degrees of freedom, n, by the number r, is not mathematically different in kind from the complete solution of the problem (the determination of the form of the unknown function, F) which is obtained when $(n - 1)$ independent transformation parameters are obtained.

3. A FORMAL SOLUTION FOR b_i^k.

Equations 2.11 are equivalent to the matrix equation

$$AB = 0, \tag{3.1}$$

where $A = \|a_j^i\|$, $B = \|b_i^k\|$. The rank of A is r; by mere rearrangement of rows and columns, the non-vanishing determinant can be made to appear in the upper right-hand corner of A (under the last r columns and the first r rows; it will be supposed that the subscript is the row index, the superscript the column index). Call this portion of the matrix A_1, call the first $(n - r)$ columns and first r rows A_2; let the last $(m - r)$ rows be called A_0 (if $r = m$, A_0 does not exist).

Make a corresponding partition of B, calling the first $(n - r)$ rows

B_2, the remaining rows B_1. Then Eq. 3.1 is equivalent to

$$\left\| \begin{array}{c|c} A_2B_2 + A_1B_1 & \\ \hline & A_0 \left\| \begin{array}{c} B_2 \\ \hline B_1 \end{array} \right\| \end{array} \right\| = 0. \tag{3.2}$$

But since the rows of A_0 are linearly dependent upon the rows of $\|A_2 \vdots A_1\|$, any solution of

$$A_1B_1 = -A_2B_2 \tag{3.3}$$

automatically makes $A_0 \left\| \begin{array}{c} B_2 \\ \hline B_1 \end{array} \right\|$ vanish. Since $|A_1| \neq 0$, A_1^{-1} exists and

$$B_1 = -A_1^{-1}A_2B_2. \tag{3.4}$$

The elements of B_2 are now completely arbitrary, and it is convenient, as will be shown below, to let B_2 equal the negative unit matrix, whence

$$B_1 = A_1^{-1}A_2. \tag{3.5}$$

Combination with Eqs. 2.10 and 2.11 gives the result that the invariants are:

$$y^k = \prod_{p=1}^{r} \frac{(x^{n-r+p})^{b^k_{n-r+p}}}{x^k}, \tag{3.6}$$

that is, since the y^k are to be held constant, the first $(n - r)$ variables must be individually proportional to a set of products involving only the last r variables which may be changed arbitrarily.

4. THE SCALING CRITERION.

In the application of these results to the design of model experiments certain difficulties arise which have not previously been considered in the general case. It frequently occurs that some of the variables essential to a given problem may not be readily changed with scale. As examples, the acceleration of gravity, or, in certain cases, even the properties of liquid and solid media cannot be readily altered in general so as to satisfy Eqs. 3.6 and must therefore be regarded as fixed. In order to set up a general criterion for determining whether scaling is possible, it will be useful to classify the variables in three types: those which are fixed, those which are to be arbitrarily (and independently) scaled, and those which are unrestricted. We shall use the subscripts f and s to designate the first two types respectively; r_s, r_f, r_{sf} will stand for the rank of the sub-matrix of A corresponding to all the variables of types s, f, and both s and f, respectively: t_s, t_f, t_{sf} will stand for the number of y^k which involve variables of type s, f, s and/or f, respectively; and n_s, n_f are the numbers of variables of type s and of type f. A neces-

sary and sufficient condition that scaling be possible is that

$$n_s + r_f = r_{sf}. \tag{4.1}$$

To prove the necessity of the condition, suppose $n_s + r_f \neq r_{sf}$. Since r_{sf} cannot exceed $n_s + r_f$, we must suppose $n_s + r_f > r_{sf}$ or $n_s + n_f - r_{sf} > n_f - r_f$, but since

$$t_{sf} = n_s + n_f - r_{sf}$$

and

$$t_f = n_f - r_f$$

we should have

$$t_{sf} > t_f$$

so that there would be either or both of the following types of y^k:

1. those containing arbitrarily scaled variables only,
2. those containing arbitrarily scaled and fixed, but not unrestricted variables,

neither of which types can be allowed.

To prove that the condition is sufficient, distinguish the two possible cases:

1. $r_{sf} = r$
2. $r_{sf} < r$.

In case (1), that part of A_{sf} with the $r_{sf} \times r_{sf}$ non-vanishing determinant can be taken as A_1; consequently (since such a determinant can be found which contains columns from all the arbitrarily scaled variables) all the arbitrarily scaled variables will appear in the set x^{n-r+p}, the fixed variables (if any) not contained in A_1 will be expressible in terms of fixed variables in A_1 only, and there will be just enough restricted variables to complete the set of $(n - r)y^k$'s with one such variable to each y^k involving arbitrarily scaled variables.

If, on the other hand, case (2) obtains, the same proof will hold (with the modification that some unrestricted variables will appear in the set x^{n-r+p}) provided only that the $r_{sf} \times r_{sf}$ non-vanishing determinant contained in A_{sf} is contained in some $r \times r$ non-vanishing determinant of A.

That this latter requirement is always satisfied follows, for example, from the definition of rank in terms of linear independence as shown by Birkhoff and MacLane (4). This completes the proof of the scaling criterion.

In concluding this section it should be remarked that the criterion furnished by Eq. 4.1 is independent of the basis of fundamental units adopted, since the only quantities appearing are numbers of variables and the rank of various sub-matrices, taken by columns, which are, of course, all invariant under the group of homogeneous linear transformations on the a_j^i, $A \to \bar{A} = TA$, $|T| \neq 0$, which corresponds to all conceivable choices of a basic set of fundamental units.

5. APPLICATION TO HYDRODYNAMICS.

Consider the dimensional composition of the variables appearing in the analytical description of fluid flow. The Navier-Stokes equation and the equation of continuity contain variables of the following dimensional types: v = velocity, p = pressure, R = any length, t = time, ρ = density, μ = viscosity. If the external forces are due to gravity, the acceleration of gravity, g, is included. In addition, there exists an equation of state which expresses ρ as a function of p alone in case the flow is assumed to be isothermal or adiabatic. The implication of this last condition is important in the consideration of possible scaling solutions: although the specific form of the equation of state is unknown, it must be expressible in terms of variables, such as the bulk modulus, whose columns in A are linear combinations of the columns in A representing ρ and p. In order to maintain, temporarily, the generality of the discussion, it will be supposed that the density is given by the series:

$$\rho = \sum_{i=\alpha}^{\omega} \rho_i (p)^i \qquad (5.1)$$

with $\alpha \leqq \omega$.
The A matrix is then as follows:

A	v	p	t	ρ_i	μ	g	R
M	0	1	0	$1-i$	1	0	0
L	1	-1	0	$-3+i$	-1	1	1
T	-1	-2	1	$2i$	-1	-2	0

A model experiment will now be considered in which R plays the role of the deliberately scaled variables: $n_s = 1$. Then the criterion of Eq. 4.1 requires $r_{sf} = r_f + 1$. If the medium is unchanged with scale, in the general case the rank of (ρ_i, μ) is 3 so that, since r_{sf} also equals 3, scaling is impossible. Even for an incompressible fluid ($\rho_i = 0$ except for $i = 0$) a scaling solution with fixed g is impossible if μ is fixed. The idealizations which lead to the familiar scaling approximations in terms of the Froude, Reynolds, and Mach numbers are described in Table I. In each case the set of variables designated as "ignored" are shown to be

TABLE I.

Scaling Laws for Hydrodynamics.

Typical Invariant	Ignorable Variables	v	p	t	ρ_i	μ	g	Fixed Variables
Froude Number	$\rho_i (i \neq 0), \mu$	$\frac{1}{2}$	1	$\frac{1}{2}$	$(-i)$	$(\frac{3}{2})$	0	ρ_0, g
Reynolds Number	$\rho_i (i \neq 0), g$	-1	-2	2	$(2i)$	0	(-3)	ρ_0, μ
Mach Number	μ, g	0	0	1	0	(1)	(-1)	ρ_i
—	$\rho_i (i \neq 0, 1), \mu$	$\frac{1}{2}$	0	$\frac{1}{2}$	$[-1]$	$(\frac{1}{2})$	0	$\frac{\rho_i}{\rho_0}, g$

required to follow rather impractical scaling laws, but by assuming that their influence on the flow is unimportant in a certain range of velocities, a solution is obtained by omitting them from further consideration. The dependence of the variables is expressed in terms of the exponent b_i^R in the expression

$$x^i = x^{io}\left(\frac{R}{R^o}\right)^{b_i^R}, \tag{5.2}$$

where x^i is the appropriate value of the ith variable on any scale with a typical length R related to the model scale with corresponding values x^{io} and R^o. The computation of the b_i^R requires only the determination of that row of A_1^{-1} which corresponds to the column of A_1 in which R appears.

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Contribution No. 394

CHARACTERISTICS OF SEA WATER

ALFRED C. REDFIELD*

DEFINITIONS

The proportions of the major constituents of natural sea water obtained from the open oceans are very uniform, the ratio of water to total salt content being the principal variant. Many properties of sea water can consequently be determined from tables if the total salt content and the temperature are defined. The quantity of any constituent may be estimated if the chlorinity (defined below) of a sample is measured. (See Tables 1 and 2.)

TABLE 1. THE MAJOR CONSTITUENTS OF SEA WATER*

Chlorinity = 19.00 0/00†

Ion	Parts per Million	Equivalents per Million	Parts per Million per Unit Chlorinity
Chloride, Cl^-	18,980.0	535.3	998.90
Sulfate, SO_4^{--}	2,649.0	55.1	139.40
Bicarbonate, HCO_3^-	139.7	2.3	7.35
Bromine, Br^-	64.6	0.8	3.40
Fluoride, F^-	1.3	0.1	0.07
Boric acid, H_3BO_3	26.0	....‡	1.37
Total		593.6	
Sodium, Na^+	10,556.1	459.0	555.60
Magnesium, Mg^{++}	1,272.0	104.6	66.95
Calcium, Ca^{++}	400.1	20.0	21.06
Potassium, K^+	380.0	9.7	20.00
Strontium, Sr^{++}	13.3	0.3	0.70
Total		593.6	

* H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942. J. Lyman and R. H. Fleming, *J. Marine Research*, **3**, 134–146, 1940.

† 0/00 is used to denote grams per kilogram or parts per thousand.

‡ Undissociated at usual *p*H.

The total salt content of sea water is frequently expressed as *salinity*. Salinity is defined as the total amount of solid material in grams contained in one kilogram of sea water when all carbonate has been converted to oxide, the bromine and iodine replaced by chlorine, and all organic matter is completely oxidized.

Because of the convenience of chlorine analysis by titration with silver nitrate, potassium dichromate being used as an indicator, the salt content of sea water is frequently expressed as *chlorinity*. Chlorinity is defined approximately as the total amount of chlorine, bromine, and iodine in grams contained in one kilogram of sea water, assuming that the bromine and the iodine have been replaced by chlorine. Since this definition depends upon the accepted values of atomic weights, which have changed since the definition was established by an international commission, in exact oceanographic work chlorinity is established by comparison with a standard "Normal Water" now prepared at the Woods Hole Oceanographic Institution.

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Contribution No. 391
from the
Woods Hole Oceanographic Institution

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TABLE 2. ELEMENTS PRESENT IN SOLUTION IN OCEANIC SEA WATER EXCLUSIVE OF DISSOLVED GASES*

Chlorinity = 19.00 0/00

Element	Parts per Million	Element	Parts per Million
Chlorine	18980	Copper	0.001–0.01
Sodium	10561	Zinc	0.005
Magnesium	1272	Lead	0.004
Sulfur	884	Selenium	0.004
Calcium	400	Cesium	0.002
Potassium	380	Uranium	0.0015
Bromine	65	Molybdenum	0.0005
Carbon	28	Thorium	0.0005
Strontium	13	Cerium	0.0004
Boron	4.6	Silver	0.0003
Silicon	0.02–4.0	Vanadium	0.0003
Fluorine	1.4	Lanthanum	0.0003
Nitrogen†	0.006–0.7	Yttrium	0.0003
Aluminum	0.5	Nickel	0.0001
Rubidium	0.2	Scandium	0.00004
Lithium	0.1	Mercury	0.00003
Phosphorus	0.001–0.10	Gold	0.000006
Barium	0.05	Radium	$0.2–3 \times 10^{-10}$
Iodine	0.05	Cadmium	present
Arsenic	0.002–0.02	Cobalt	present
Manganese	0.001–0.01	Tin	present

* H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942.

† Nitrogen in combined forms.

TABLE 3. CHLORINITY, SALINITY, AND SPECIFIC GRAVITY OF SEA WATER*

Chlorinity, 0/00	Salinity, 0/00	Specific Gravity at 17.5° C	Chlorinity, 0/00	Salinity, 0/00	Specific Gravity at 17.5° C
0.00	0.00	1.00 000			
1.00	1.84	0 144	12.00	21.69	1.01 658
2.00	3.64	0 283	13.00	23.50	1 795
3.00	5.45	0 421	14.00	25.30	1 933
4.00	7.25	0 558	15 00	27.11	1.02 070
5.00	9.06	1.00 696	16 00	28.91	2 208
6.00	10.86	0 834	17.00	30.72	2 346
7.00	12.67	0 971	18.00	32.52	2 484
8.00	14 47	1 109	19.00	34.33	2 622
9.00	16 28	1 246	20.00	36.13	1.02 760
10.00	18.08	1.01 383	21.00	37.94	2 899
11.00	19.89	1 521	22.00	39.74	3 037

* For more complete tables see M. Knudsen, *Hydrographical Tables*, 63 pp., Copenhagen, 1901, or N. N. Subow, *Oceanographical Tables*, 208 pp., Moscow, 1931.

Salinity is related to chlorinity as follows:

$$\text{Salinity} = 0.03 + 1.805 \times \text{chlorinity} \quad (1)$$

Where great precision is not required, chlorinity or salinity may be obtained conveniently from a measurement of specific gravity (Table 3) or density (Table 4), using a hydrometer. Measurements of refractive index or conductivity are applicable where special circumstances warrant the use of more elaborate apparatus.

In the open sea, the salinity varies between 32 and 36 0/00 (chlorinity 18 and 20 0/00), depending upon geographical position. In order to state rough working rules relative to its properties, *natural sea water* may be considered to have a chlorinity of approximately 19 0/00 (salt content 3.4%). Slightly higher values are found in the oceanic waters of subtropical regions. Extreme values of salinity are found in enclosed seas subject to high evaporation (Mediterranean, 38.6 0/00; Red Sea, 41 0/00). Coastal waters and tide-swept harbors are usually characterized by slightly lower salinities. Enclosed bodies of water with extensive land drainage, such as the Baltic Sea and Chesapeake Bay, have very much lower salinities, and all degrees of dilution are to be expected in the tidal estuaries of rivers.

TABLE 4. DENSITY OF SEA WATER*

As a Function of Temperature and Salinity

Salinity, Parts per Thousand	Temperature, °C							
	0	5	10	15	17.5	20	25	30
0	0.99987	1.00000	0.99973	0.99913	0.99870	0.99813	0.99707	0.99567
5	1.00397	0401	1.00367	1.00301	1.00257	1.00207	1.00086	9943
10	0801	0796	0756	0684	0638	0585	0461	1.00314
15	1204	1191	1144	1067	1019	0964	0836	0686
20	1.01606	1.01585	1.01532	1.01449	1.01399	1.01341	1.01210	1.01057
25	2008	1980	1920	1832	1779	1720	1585	1429
30	2410	2374	2308	2215	2160	2099	1960	1801
35	2813	2770	2698	2600	2542	2479	2337	2176
40	1.03216	1.03166	1.03088	1.02985	1.02925	1.02860	1.02715	1.02551

* For more complete tables see M. Knudsen, *Hydrographical Tables*, 63 pp., Copenhagen, 1901, or N. N. Subow, *Oceanographical Tables*, 208 pp., Moscow, 1931.

PHYSICAL PROPERTIES RELATED TO CHLORINITY

FREEZING POINT (TABLE 5)

The freezing point is given as the temperature of the initial formation of ice. As soon as any ice is formed, the concentration of dissolved solids increases, and the formation of additional ice takes place only at a lower temperature.

TEMPERATURE OF MAXIMUM DENSITY

Unlike fresh water, natural sea water continues to increase in density as it cools and freezes at temperatures above that of maximum density (Table 5). The transition in behavior comes at a salinity of 24.7 0/00 (chlorinity = 13.7 0/00). At lower salinities, the temperature of maximum density occurs above the freezing point, and the behavior resembles fresh water.

Osmotic Pressure, OP_0

It may be estimated from the freezing point depression, $\Delta\theta_f$ (Table 5), by the equation:

$$OP_0 = 12.08\Delta\theta_f$$

Table 5. PROPERTIES OF SEA WATER OF DIFFERENT SALINITY*

Salinity, 0/00	Freezing Point, °C	Temperature of Maximum Density, °C	Osmotic Pressure, Atmospheres	Specific Heat
0	0.00	3.95	0	1.00
5	−0.27	2.93	3.23	0.982
10	−0.53	1.86	6.44	0.968
15	−0.80	0.77	9.69	0.958
20	−1.07	−0.31	12.98	0.951
25	−1.35	−1.40	16.32	0.945
30	−1.63	−2.47	19.67	0.939
35	−1.91	−3.52	23.12	0.932
40	−2.20	−4.54	26.59	0.926

* N. N. Subow, *Oceanographical Tables*, 208 pp., Moscow, 1931. T. G. Thompson, "The Physical Properties of Sea Water," *Bull.* 85, "Physics of the Earth. V. Oceanography," p. 63, National Research Council of the National Academy of Sciences, Washington, 1932.

The osmotic pressure at any temperature, θ, is given by

$$OP = OP_0 \times \frac{273 + \theta}{273} \qquad (2)$$

The osmotic pressure of natural sea water is of the order of 20 atmospheres.

Vapor Pressure

The vapor pressure, ϵ, of sea water of any chlorinity may be estimated from the vapor pressure of distilled water, ϵ_0, by the equation:

$$\frac{\epsilon}{\epsilon_0} = 1 - 0.00969 \times \text{chlorinity} \qquad (3)$$

Roughly speaking, the vapor pressure is reduced 0.1% per 1 0/00 chlorinity. The vapor pressure of natural sea water is about 2% lower than that of fresh water.

Electrical Conductivity

For a rough working rule, the resistance of natural sea water may be taken as one ohm per foot cubed. Exact values of the specific conductance of sea water as a function of temperature and chlorinity are given in Table 6.

TABLE 6. SPECIFIC CONDUCTANCE OF SEA WATER AS A FUNCTION OF TEMPERATURE AND CHLORINITY*

Conductance in reciprocal ohm-centimeters

Chlorinity, Parts per Thousand	Temperature, °C					
	0	5	10	15	20	25
1	0.001839	0.002134	0.002439	0.002763	0.003091	0.003431
2	0.003556	0.004125	0.004714	0.005338	0.005971	0.006628
3	0.005187	0.006016	0.006872	0.007778	0.008702	0.009658
4	0.006758	0.007845	0.008958	0.010133	0.011337	0.012583
5	0.008327	0.009653	0.011019	0.012459	0.013939	0.015471
6	0.009878	0.011444	0.013063	0.014758	0.016512	0.018324
7	0.011404	0.013203	0.015069	0.017015	0.019035	0.021121
8	0.012905	0.014934	0.017042	0.019235	0.021514	0.023868
9	0.014388	0.016641	0.018986	0.021423	0.023957	0.026573
10	0.015852	0.018329	0.020906	0.023584	0.026367	0.029242
11	0.017304	0.020000	0.022804	0.025722	0.028749	0.031879
12	0.018741	0.021655	0.024684	0.027841	0.031109	0.034489
13	0.020167	0.023297	0.026548	0.029940	0.033447	0.037075
14	0.021585	0.024929	0.028397	0.032024	0.035765	0.039638
15	0.022993	0.026548	0.030231	0.034090	0.038065	0.042180
16	0.024393	0.028156	0.032050	0.036138	0.040345	0.044701
17	0.025783	0.029753	0.033855	0.038168	0.042606	0.047201
18	0.027162	0.031336	0.035644	0.040176	0.044844	0.049677
19	0.028530	0.032903	0.037415	0.042158	0.047058	0.052127
20	0.029885	0.034454	0.039167	0.044114	0.049248	0.054551
21	0.031227	0.035989	0.040900	0.046044	0.051414	0.056949
22	0.032556	0.037508	0.042614	0.047948	0.053556	0.059321

* B. D. Thomas, T. G. Thompson, and C. L. Utterback, *J. du conseil*, **9**, 28–35 (1934).

CHEMICAL PROPERTIES RELATED TO CHLORINITY

SOLUBILITY OF GASES

The concentration of a gas dissolved in a liquid is directly proportional to the partial pressure of the gas in the saturating gas phase. Table 7 gives the coefficients of saturation of oxygen, nitrogen, and carbon dioxide in sea water at different temperatures and chlorinities. The coefficients are defined as the concentrations of gas in equilibrium with one atmosphere (760 mm) of the pure gas. The values for carbon dioxide represent the amount of free CO_2 and H_2CO_3 dissolved and do not include considerable quantities of CO_2 present as bicarbonate.

The composition of the normal atmosphere with which surface waters are approximately saturated is given in Table 8.

TABLE 7. COEFFICIENTS OF SATURATION OF ATMOSPHERIC GASES IN WATER*

Concentrations of Oxygen, Nitrogen, and Carbon Dioxide in Equilibrium with 1 Atmosphere (760 mm) of Designated Gas

Gas	Chlorinity, 0/00	Temperature, °C	Concentration	
			Milliliters per Liter	Parts per Million
Oxygen	0	0	49.2†	70.4
		12	36.8	52.5
		24	29.4	42.1
	16	0	40.1	56.0
		12	30.6	42.9
		24	24.8	34.8
	20	0	38.0	52.8
		12	29.1	40.4
		24	23.6	32.9
Nitrogen	0	0	23.0†	28.8
		12	17.8	22.7
		24	14.6	18.3
	16	0	15.0	18.4
		12	11.6	14.2
		24	9.36	11.5
	20	0	14.2	17.3
		12	11.0	13.4
		24	8.96	10.9
Carbon dioxide‡	0	0	1715†	3370
		12	1118	2198
		24	782	1541
	16	0	1489	2860
		12	980	1888
		24	695	1342
	20	0	1438	2746
		12	947	1814
		24	677	1299

* Calculated from data in H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942.

† These values differ slightly from those given in Table 12, p. 1146, for fresh water.

‡ Includes CO_2 present as H_2CO_3 but not as HCO_3^- or CO_3^{--}

Atmospheric gases are present in ocean water in approximately the following quantities:

	Milliliters per liter	*Parts per million*
Oxygen	0– 9	0– 12
Nitrogen	8–15	10– 18
Carbon dioxide*	33–56	64–107
Argon	0.2–0.4	0.4–0.7
Helium and neon	1.7×10^{-4}	0.3×10^{-4}†

* Includes CO_2 present as H_2CO_3, HCO_3^- and CO_3^{--}.

† Estimated as helium.

Hydrogen sulfide is normally absent but may reach concentrations of 22 ml per liter or 33 ppm under exceptional conditions.

TABLE 8. COMPOSITION OF NORMAL ATMOSPHERE*

Gas	Volume or Pressure, %	Partial Pressure, mm Hg, 1 atm Total Pressure
Nitrogen	78.03	593.02
Oxygen	20.99	159.52
Argon	0.94	7.144
Carbon dioxide	0.03	0.228
Hydrogen, neon, helium	0.01	0.088
	100.00	760.000

* From H. U. Sverdrup, M. W. Johnson and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942.

Table 9 gives the quantity of oxygen dissolved in sea water at different temperatures and chlorinities when in equilibrium with a normal atmosphere saturated with water vapor. It thus represents the condition approached by the surface water when biological activity is not excessive.

TABLE 9. OXYGEN DISSOLVED IN SEA WATER IN EQUILIBRIUM WITH A NORMAL ATMOSPHERE (760 MM) OF AIR SATURATED WITH WATER VAPOR*

Parts per Million

Chlorinity 0/00	0	5	10	15	20
Salinity 0/00	0	9.06	18.08	27.11	36.11
Temperature °C					
0	14.62†	13.70	12.78	11.89	11.00
5	12.79	12.02	11.24	10.49	9.74
10	11.32	10.66	10.01	9.37	8.72
15	10.16	9.67	9.02	8.46	7.92
20	9.19	8.70	8.21	7.77	7.23
25	8.39	7.93	7.48	7.04	6.57
30	7.67	7.25	6.80	6.41	5.37

* Based on data of C. J. J. Fox, Conseil permanent international pour l'exploration de la mer, Copenhagen, *Publication de circonstance* 41 (1907).

† The values for solubility in water of zero chlorinity differ slightly from those given in Table 12, p. 1146, for fresh water.

Detailed tables on the solubility of nitrogen in sea water are available.[1,2]

ALKALINITY

In oceanographic chemistry, alkalinity is defined as the number of milliequivalents of hydrogen ions necessary to combine with the ions of weak acids in a quantity of

[1] C. J. J. Fox, Conseil permanent international pour l'exploration de la mer, Copenhagen, *Publication de circonstance* 41 (1907).

[2] N. W. Rakestraw and V. M. Emmel, *J. Phys. Chem.*, **42**, 1211 (1938).

water which at 20° C has a volume of one liter. Thus it represents approximately the concentration of bicarbonate and carbonate ions present.

The alkalinity of ocean water is related fairly closely to chlorinity by the expression:

$$\text{Alkalinity} = 0.120 \times \text{chlorinity} \times \rho_{20}$$

where ρ_{20} is the density of the water at 20° C. Departures from this ratio are usually attributed to changes in the calcium carbonate content of sea water, such as result from biological activity or the dilution of sea water with river water rich in calcium carbonate. Alkalinity may also be used as an index of pollution by acid or basic materials. There are several methods of determining alkalinity.[3,4,5]

Hydrogen-Ion Concentration

Owing to the excess of strong basic ions, pure sea water is slightly alkaline. The *p*H of sea water in equilibrium with the air varies between 8.1 and 8.3. The removal of carbon dioxide by photosynthetic processes of marine plants increases the *p*H somewhat, an exceptional limiting value observed being as great as 9.7. The decomposition of organic matter in water removed from the influence of the atmosphere decreases the *p*H. Values as low as 7.5 are observed at certain depths in the Pacific, where decomposition has almost entirely removed the dissolved oxygen. In stagnant basins where large amounts of H_2S are present, the *p*H may approach 7.0.

The carbonates constitute the principal buffer system of sea water. Boric acid is also present in small amounts (0.43 mg moles/liter) but is almost completely undissociated at commonly existing *p*H. The buffer capacity of sea water is equal to the *alkalinity*. When strong base is added, magnesium hydrate is precipitated at *p*H values between 10 and 11, and higher *p*H values are not obtained until the considerable quantity of magnesium present is exhausted. Calcium is precipitated in a similar way at higher *p*H values.

There are tables giving the *p*H and total CO_2 content of sea water in equilibrium with various pressures of CO_2 at different temperatures and chlorinities.[6]

Solubility of Salts

Because of the influence of other ions upon the activity of a given ion, the solubility product of salts in distilled water cannot be applied to sea water. The solubility products of several salts in distilled water and in sea water of salinity 35 0/00 at 20° C are compared in Table 10.

The solubility product of calcium carbonate given in Table 10 is less than the product of the concentration of calcium and carbonate ions in natural sea water (270×10^{-8} at *p*H 8.2), which indicates that sea water is supersaturated in respect to this salt. Because some uncertainty exists in the matter, the original studies should be consulted.[7,8,9]

[3] D. M. Greenberg, E. G. Moberg, and E. C. Allen, *Ind. Eng. Chem.*, Anal, Ed., **4**, 309 (1932).

[4] P. H. Mitchell and N. W. Rakestraw, *Biol. Bull.*, **65**, 437 (1933).

[5] S. Grippenberg, International Association of Physical Oceanography (Association d'Océanographie physique, Union Géodesie et Géophysique, internationale, *Rapport et procès-verbal*, No. 2, p. 150, Liverpool (1937).

[6] K. Buck, H. W. Harvey, H. Wattenberg, and S. Grippenberg, "Über das Kohlensauresystem in Meerwasser," Conseil permanent international pour l'exploration de la mer, *Rapport et procès-verbal*, **79** (1932).

[7] H. Wattenberg and E. Timmermann, *Ann. Hydrog. u. Mar. Meteor.*, **64**, 23–31 (1936) and *Kieler Meeresforschung*, **2**, 81–94 (1938).

[8] R. Revelle and R. H. Fleming, Fifth Pacific Scientific Congress, Canada, 1933, *Proc.*, **3**, 2089–2092 (1934).

[9] R. Revelle, *J. Sedim. Petrol.*, **4**, 103–110 (1934).

TABLE 10. SOLUBILITY PRODUCTS OF CERTAIN SALTS IN DISTILLED WATER AND IN SEA WATER OF SALINITY 35 0/00 AT 20° C*

Salt	Distilled Water	Sea Water
$CaCO_3$	0.5×10^{-8}	50×10^{-8}
$MgCO_3 \cdot 3H_2O$	0.1×10^{-4}	3.1×10^{-4}
$SrCO_3$	0.3×10^{-9}	500×10^{-9}
$Mg(OH)_2$	1×10^{-11}	5×10^{-11}

* From H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942.

Calcium carbonate becomes less soluble under conditions which increase the temperature or *p*H of sea water. Calcium and magnesium carbonates and hydroxides are precipitated on cathodic surfaces, as in cathodic protection and in galvanic couples, as the result of induced increases in the ionic products at the electrode.

The presence of calcium and magnesium introduces special difficulties when sea water is treated with many substances owing to the tendency of these ions to form relatively insoluble compounds.

CHEMICAL SUBSTANCES INFLUENCED BY ORGANIC ACTIVITY

A number of substances present in sea water are absorbed by growing plants and are set free by the decomposition of organic matter. Their concentrations are consequently widely variable and are related to the seasonable cycle of biological activity. Pollution with domestic sewage or organic wastes, and the resulting bacterial activity, increases the concentration of these materials in sea water.

The growth of marine plants may almost completely remove the phosphates and nitrates from sea water during the late spring and summer. The silicate concentration may be greatly reduced, and because of the absorption of CO_2 in photosynthesis, the *p*H is increased slightly. Photosynthesis may produce sufficient oxygen to increase the oxygen content in the subsurface water 10 to 20% above the saturation value. During the fall and winter in the surface layers of the sea, processes of decomposition predominate, higher values of nitrate, phosphate, and silicon are to be expected, and the oxygen content of the water is very nearly in equilibrium with the air.

In deep water this is also true at all seasons except that the oxygen content is reduced by the oxidation of organic matter and falls below the saturation value.

In tropical waters the seasonal cycle is less pronounced, and the surface waters remain depleted of phosphate and nitrate throughout the year.

The range in concentration of the various inorganic forms of nitrogen and of phosphate phosphorus to be encountered in natural (unpolluted) sea water are:

Nitrogen as NO_3	0.001 –0.6 ppm
Nitrogen as NO_2	0.0001–0.05 ppm
Nitrogen as NH_3	0.005 –0.05 ppm
Phosphorus as PO_4	0.001 –0.10 ppm

Pollution with domestic sewage or organic wastes increases the concentration of organic derivatives, i.e., nitrogen compounds and phosphates, in the sea water, and may result in a marked deficiency in the oxygen content. If the pollution is sufficiently intense to result in anaerobic conditions, the activity of bacteria may result in the

production of hydrogen sulfide consequent to the reduction of sulfates. Conditions of this kind occur commonly in the muds of polluted regions where organic debris tends to accumulate.

In the decomposition of nitrogenous matter, ammonia is liberated initially. It is first oxidized to nitrite and subsequently to nitrate. The presence of unusual quantities of ammonia and nitrite may consequently be taken as signs of recent active pollution.

WATER OF ESTUARIES

The dissolved solids of river water differ in composition from those of sea water (Table 11). Consequently where sea water is mixed with considerable quantities of river water, the concentration of various constituents cannot be estimated precisely

TABLE 11. PERCENTAGE COMPOSITION OF DISSOLVED SOLIDS IN SEA WATER AND RIVER WATER*

Substance	Sea Water	River Water Weighted Average	Mississippi River	Columbia River	Colorado River
CO_3^{--}	0.41 (HCO_3^-)	35.15	34.98	36.15	13.02
SO_4^{--}	7.68	12.14	15.37	13.52	28.61
Cl^-	55.04	5.68	6.21	2.82	19.92
NO_3^-	....	0.90	1.60	0.49	....
Ca^{++}	1.15	20.39	20.50	17.87	10.35
Mg^{++}	3.69	3.41	5.38	4.38	3.14
Na^{++}	30.62	5.79	8.33	8.12	19.75
K^+	1.10	2.12	....	1.95	2.17
$(Fe,Al)_2O_3$	....	2.72	0.58	0.08	....
SiO_2	....	11.67	7.05	14.62	3.04
Sr^{++},H_3BO_3, Br^-	0.31	....	....	....	....
Salt content, ppm	35,000	....	166	92.4	702

* H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans*, Prentice-Hall, Inc., New York, 1942. F. W. Clarke, U. S. Geological Survey, *Bull.* 770, 5th Ed., 841 pp. (Washington, D. C., 1924).

from the chlorinity. River water is usually relatively richer in calcium carbonate in particular, and also in magnesium, potassium, sulfate, iron, and silicon. It is for this reason that the salinity of sea water is not exactly proportional to the chlorinity, as shown by relation 1 (p. 1113). In harbors and estuaries, the proportions of the constituents may be further disturbed by pollution. When this is of domestic origin or contains organic wastes, the tendency is toward a decrease in oxygen content and *p*H and an increase in nitrogenous compounds, particularly ammonia, and of sulfur as sulfide.

Where river water mixes with sea water there is frequently a tendency for stratification to develop, the fresh water flowing out over the salt water which lies at greater depth. Under such circumstances examination of samples collected from the surface will give incomplete information, and marked changes in salinity may accompany the tidal cycle.

ARTIFICIAL SEA WATER

For experimental work where the physical properties of sea water, such as osmotic pressure or electrical conductivity, are at issue a 3.4% solution of sodium chloride may be used. Where the action of the water to be examined is of a chemical nature a more exact reproduction of sea water is desirable, depending upon the nature of the problem. Formulas for artificial sea water are given in Table 12. Preparations of natural sea salt may also be employed.

TABLE 12. FORMULAS FOR ARTIFICIAL SEA WATER

Chlorinity = 19.00 0/00

Naval Aircraft Factory Process Specification PS-1 for synthetic sea water, for use in testing corrosion-resisting steel tubing (Navy Department Specification 44T27b, dated July 1, 1940), is as follows:

Stock Solution

Potassium chloride	10 grams
Potassium bromide	45 grams
Magnesium chloride	550 grams
Calcium chloride	110 grams
Sterile distilled water to make 1 liter	

This stock solution is used with other chemicals to make the synthetic sea water as follows:

Sodium chloride — NaCl	23 grams
Sodium sulfate — $Na_2SO_4 \cdot 10H_2O$	8 grams
Stock solution	20 ml
Sterile distilled water to make 1 liter	

Other recommended compositions are as follows:

McClendon *et al* (1917)*		Brujewicz (Subow, 1931)†		Lyman and Fleming (1940)‡	
Salt	grams/kg	Salt	grams/kg	Salt	grams/kg
NaCl	26.726	NaCl	26.518	NaCl	23.476
$MgCl_2$	2.260	$MgCl_2$	2.447	$MgCl_2$	4.981
$MgSO_4$	3.248	$MgSO_4$	3.305	Na_2SO_4	3.917
$CaCl_2$	1.153	$CaCl_2$	1.141	$CaCl_2$	1.102
KCl	0.721	KCl	0.725	KCl	0.664
$NaHCO_3$	0.198	$NaHCO_3$	0.202	$NaHCO_3$	0.192
NaBr	0.058	NaBr	0.083	KBr	0.096
H_3BO_3	0.058			H_3BO_3	0.026
Na_2SiO_3	0.0024			$SrCl_2$	0.024
$Na_2Si_4O_9$	0.0015			NaF	0.003
H_3PO_4	0.0002				
Al_2Cl_6	0.013				
NH_3	0.002				
$LiNO_3$	0.0013				
Total:	34.4406		34.421		34.481
Water to:	1,000.0000		1,000.000		1,000.000

* J. F. McClendon, C. C. Gault, and S. Mulholland, Carnegie Institution of Washington, *Publication* 251 (Papers from Dept. of Marine Biology), pp. 21–69 (1917).

† N. N. Subow, *Oceanographical Tables*, U. S. S. R. Oceanographic Institute Hydro-Meteoral Com. 208 pp. Moscow, 1931.

‡ J. Lyman and R. H. Fleming, *J. Marine Research*, **3**, 134–146 (1940).

It should not be assumed that the results of corrosion tests in any synthetic sea water may be applied directly to an estimation of the performance of materials under natural conditions of exposure to sea water.

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Contribution No. 395

THE DISTRIBUTION OF LARGER PLANKTONIC CRUSTACEA ON GEORGES BANK

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THE DISTRIBUTION OF LARGER PLANKTONIC CRUSTACEA ON GEORGES BANK

INTRODUCTION

Factors contributing to the productivity of Georges Bank, an extensive and important fishing area east of Cape Cod, were investigated from September 1939 to June 1941. Stations occupied and general hydrographic conditions that existed during the eleven cruises have already been described (Clarke, Pierce, & Bumpus 1943). The present paper now discusses the plankton collections made by the 1.5 meter stramin net with special reference to the larger Crustacea such as amphipods, euphausiids, mysids and decapods.

A number of investigators (Smith & Verril 1873; Bigelow 1926; Needler 1930) have found that with the possible exception of the bottom feeding haddock several commercially important fish of Georges Bank, such as mackerel, herring, and even cod, though perhaps to a lesser extent than the others, depend on the larger Crustacea or their larvae for much of their food. Hence the larger Crustacea can be considered important in the food cycle of Georges Bank.

Excepting the cruise of January, 1940, these larger Crustacea constituted more than half the volume of the stramin net hauls in 60% to 80% of the cases for each cruise. This volumetric abundance of the plankton is presently described. Species composition of the larger Crustacea, the occurrence of predominating species, and effects of the physical factors on distribution are also presented and the results analyzed.

I am greatly indebted to the Woods Hole Oceanographic Institution for making this investigation possible, and take great pleasure in thanking Dr. George L. Clarke for his unfailing interest and helpful counsel. I am also indebted to Dr. Alfred C. Redfield for criticism of the manuscript. Acknowledgment of courtesies is also due Dr. C. R. Shoemaker and Dr. W. L. Schmitt of the National Museum for assistance in the identification of several species and to Mr. Dean F. Bumpus of the Woods Hole Oceanographic Institution, who supervised the collection of the plankton on Georges Bank and examined the plankton sampler tows.

COLLECTION AND ANALYSIS OF DATA

A stramin net (diameter: 1.5 m., mesh 6 strands per cm.) with a 1.0 m. No. 00 silk inner tail (11 strands/cm.) was used. An outside ring, to which was fitted wooden rollers, was attached to the net ring in order that the net could be safely towed as deeply as possible without fouling if it should strike bottom. The net was lowered until its edge touched bottom or, as in deep water, beyond the edge of the bank, to a maximum depth of 200 meters. It was subsequently raised so as to make an oblique tow of from 30 minutes to 80 minutes. The steps by which the net was raised were as follows:

At stations with depth of 35-50m. net was raised 5 m. every 4 minutes.
At stations with depth of 50-75 m. net was raised 5 m. every 3 minutes.
At stations with depth of 75-100 m. net was raised 5 m. every 2 minutes.
At stations with depth of 100-150 m. net was raised 5 m. every 1.5 minutes.
At stations with depth of 150-200 m. net was raised 5 m. every 1.0 minutes.

Data which would represent the whole area as accurately as possible were obtained by covering Georges Bank with a net-work of stations 10-20 miles apart. The towing speed for the stramin net hauls averaged 2 knots or 61.7 meters per minute. On this basis the linear extent of a tow of 30 minutes would be 1851 meters or about a mile. Since duration of the tows varied, results were expressed by the number of individuals per 1000 revolutions of a flow meter which was fitted in the mouth of the net to determine the relative amount of water passing through. Hauls reduced to this basis are termed standard hauls in the present report.

By the use of the flow meter it is possible to express results on a relatively quantitative basis even though speed of the ship unavoidably varied and the net probably clogged to different degrees under different conditions. Nevertheless, the actual amount of water filtered during the standard haul is not known because of water lost owing to backwash from the mouth of the net. An approximate value may be reached, however, by comparison with the number of organisms caught at the same stations by Clarke plankton samplers (Clarke & Bumpus 1940) for which the volume of water filtered is accurately known, since each instrument is provided with a propeller geared to a cyclometer which thus measures the volume of water that has passed through the net. Since the plankton samplers rarely caught large numbers of the crustaceans taken by the stramin net, conversion factors were obtained from another part of the investigation where ample numbers of fish larvae were taken in nets of both types.

Use of these factors showed that the amount of water actually passing through the stramin net during 1000 revolutions of the flow meter varied between 150 and 500 cubic meters or had an approximate average volume of 300 cubic meters. This variation was apparently due to difference in meters used from

cruise to cruise and in the exact orientation of the meter in relation to water passing through the net.

These volumes may be compared with the theoretical amount which would result if all water was filtered by the stramin net towed for 30 minutes at 2 knots. The volume of the cylinder 1851 meters in length and 1.5 meters in diameter would be 3258 m^3. The average number of revolutions for a 30 minute tow has been found to reach 3600. Hence the maximum value corresponding to 1000 revolutions of the flow meter would be 905 $m.^3$ for 100% filtering efficiency. Since the values obtained from the fish larvae study showed that between 150 and 500 $m.^3$ were actually filtered, a working efficiency of the stramin net of between 16% and 55% may be obtained.

One thus has an approximate idea of the amount of water filtered by the standard stramin haul. It is unfortunate that there may have been a threefold variation in this value but since in most cases the abundance of the plankton varies by a much greater amount, the results can be regarded as being on a quantitative basis.

For each station, either the whole sample or several parts, each not less than 10%, of the sample were examined. All amphipods, mysids, euphausiids, and decapods in the plankton were identified and counted and the number per standard haul was calculated.

Since vertical distribution of the larger Crustacea is not readily determined by stramin net, Clarke plankton samplers were used to provide these data. The sampler is equipped with a shutter, hence while being towed, its mouth can be opened or closed. In this way a single instrument can be used to sample separate levels of the water column, one at a time, or a series of samplers to be opened and closed at desired depths can be towed simultaneously. The terms "Shallow," "Second-depth" and "Deep," introduced by Clarke, Pierce, & Bumpus (1943), will describe the strata fished by the plankton samplers when vertical distribution of the Crustacea is discussed. The depths of the water that corresponded to the strata were as follows:

Stratum	*Water less than 75 m.*	*Water more than 75 m.*
"Shallow"	0 m. to 25 m.	0 m. to 25 m.
"Second-depth"	25 m. to bottom	25 m. to half-distance to bottom (or to half-distance to 200 m.)
"Deep".		Remaining distance to bottom (or to 200 m.)

PHYSICAL CONDITIONS

Georges Bank (Fig. 1) is an elongated submarine plateau with a steep north-western face towards the Gulf of Maine and a gradual south-eastward tilt in the direction of the Continental Slope. The plateau is about 150 miles long and 100 miles wide. Depth of water varies from 200 m. at the edge of the bank to 5 m. on Georges Shoal in the northwest section. The depth of the major portion of the bank lies between 40 and 100 m.

Turbulence caused by tidal currents and winds results in vertical mixing of a large amount of the relatively shallow water overlying the bank. The mixing produces in this water mass a nearly uniform distribution of temperature and salinity from surface to bottom at all seasons of the year (Clarke, Pierce, & Bumpus 1943). That portion of Georges Bank over which nearly complete mixing is found has been called by these investigators the "Mixed Area"; all stations at which the salinity does not vary by more than 0.2 part per mille from surface to bottom are considered to lie within it and its position is shown on the distribution charts (Figs. 3-10) by a heavy broken line. The bank water of the Mixed Area thus contrasts sharply with the surrounding water masses which are typically stratified during all except the winter months.

Water temperatures in the Mixed Area vary less than 1.6° C. from surface to bottom and salinity changes less than 0.2‰. While these variations are not considered ecologically important as far as temperature tolerance is concerned a vertical gradient, even of 1.6° C., tends to create stability. Hence planktonic crustaceans cannot be carried by mixing from surface to bottom but have to pass through intermediate layers. Lateral mixing may occur in the intermediate layers. Turbulence expresses itself as lateral mixing in the presence of stability. Within the Mixed Area, wherever water is perfectly homogeneous, distribution of plankton is governed by vertical mixing or upwellings freely following tidal circulation and the disturbing effects which wind exercises on the surface. Since the larger Crustacea are caught both inside and outside of the Mixed Area and as they are believed to be species characteristic of mid-depth or bottom an examination of the effects of bottom temperatures on distribution will be discussed later in this paper.

In Table 1, bottom temperatures at stations within the 100 m. contour and at stations between the 100 m. and 200 m. contours are given for 1940 and 1941. The stations on the north edge of the bank between the 100 m. and 200 m. contours have been listed separately from those on the south edge of the bank in order to show differences that may exist between these two regions. The bottom temperatures of the north edge of the bank would be influenced by the mixing of bank water with generally cooler Gulf of Maine water, whereas the south edge of the bank would have bottom temperatures resulting from a mixing of bank water with warmer Atlantic slope water. For these reasons, the maximum and minimum values only for the bottom temperatures between 100 m. and 200 m. are given in Table 1. Average bottom temperatures for these deep stations would have little significance. Bottom temperatures at all stations inside the 200 m. contour for the six cruises are found in Figure 2. For stations off the bank the temperatures are for 200 meters.

Examination of Table 1 and Figure 2 shows that within the 100 m. contour average bottom temperatures may vary seasonally from 3° C. to 12° C.; within the 100 m. to 200 m. contours the same range of actual—not average—temperatures may be found

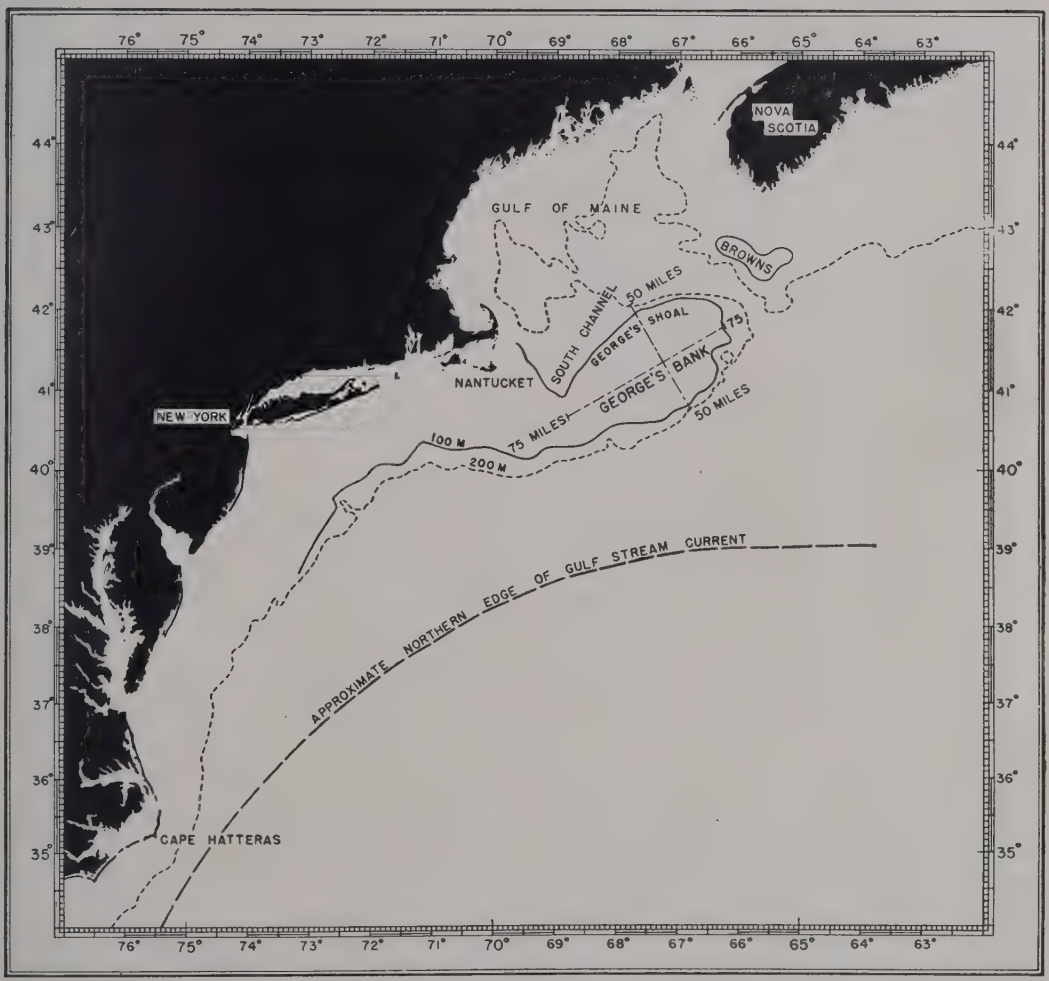

FIG. 1. Orientation map of Atlantic Coast. The location and size of Georges Bank are indicated.

when both the north and south edges of the bank are considered. Bottom water of the bank is warmest in September; within the 100 m. contour the average temperature is then warmer by approximately 3° C. than the maximum temperature of the deeper water. This condition is most probably the effect of solar heating and the transfer of warm surface water to the bottom by vertical mixing. Coolest bottom water temperatures are found in March and April. During winter Georges Bank water is colder than either Gulf or Maine or Atlantic slope water. Effect of winter cooling and summer heating is more pronounced in the well-mixed shoaler water. Warm slope water appears to have an influence on the bottom temperatures of the southern section of Georges Bank within the 100 m. to 200 m. contours since maximum temperatures of approximately 12° C. occur here as early as March. Cold water from the Gulf of Maine appears to influence bottom temperatures on the northern section of the bank because the highest temperature recorded here was approximately 6° C.

The water in the Mixed Area is believed to be relatively stationary, that is, there is little movement across it except perhaps during winter (Bigelow 1926). Around the northern, eastern, and southern margins of the bank, there is a well established clockwise current. Anomalous conditions occur from time to time along the edge of the bank probably influenced by this current. For example, during spring and summer on the southern seaward side of the bank, a tongue of cold water dovetails in between the warmer and fresh bank water on the north and the Gulf Stream on the south. This tongue, observed by Bigelow in 1924, and also during the present investigation, may serve to transfer Gulf of Maine water and its plankton on to Georges Bank (Clarke, Pierce, & Bumpus 1943).

Presumably fuana of the Mixed Area can reach

TABLE 1. Bottom temperatures at stations within the 100-meter contour and at stations between the 100-meter and 200-meter contours for 1940 and 1941. Stations on the north edge and south edge listed separately for purpose of comparison. Temperatures given in degrees centigrade.

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	16.2	6.0	3.9	4.3	5.8	8.2	10.2	3.9	4.9	6.0	8.0
Minimum	5.4	4.1	2.3	3.4	3.8	4.3	5.7	2.4	2.9	3.8	4.1
Average	11.5	4.7	2.8	3.6	4.7	6.2	7.4	3.0	3.9	4.9	6.2

BOTTOM TEMPERATURES AT STATIONS BETWEEN THE 100 M. AND 200 M. CONTOURS

NORTH EDGE OF BANK

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June 11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	4.9	5.2	3.2	4.0	5.8	4.6	4.8	4.3	5.2	4.7	4.5
Minimum	4.6	5.1	2.6	3.0	3.0	2.9	3.0	3.6	4.0	4.4	4.4

SOUTH EDGE OF BANK

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June 11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	9.4	6.0	11.5	11.2	8.1	10.3	10.8	11.7	5.2	8.6	7.7
Minimum	7.6	5.7	3.2	4.0	4.2	4.9	5.1	4.8	4.7	3.8	4.3

markedly different physical conditions only by migrating laterally out of it. Iselin (1939) has drawn attention to the possibility of lateral turbulence as a factor in the transport of plankton. When vertical stability is high, lateral turbulence is active (Parr 1936), hence the possibility of lateral transport of plankton on to Georges Bank from its margins or vice versa may be expected during early autumn, when conditions favoring stability usually prevail. But the intermingling of surrounding water with the Mixed Area is probably a slower process, and the degree to which the movements of crustacea during September within the Mixed Area is influenced by this transport is not yet clear. Study of the distribution of the larger Crustacea has on the whole not added to knowledge concerning the circulation over Georges Bank. Since these organisms can migrate vertically or even perhaps rest on the bottom for considerable periods they are inferior to more passive types as current indicators. Little is known about the nature of the bottom surface or the bottom fauna of Georges Bank. Dredging was carried on at 15 stations by Smith & Harger in 1874 and since then random bottom samples have been collected by the United States Coast and Geodetic Survey while making soundings on the bank. About thirty photographs of the bottom were made by automatic underwater cameras during the present investigation by members of the Oceanographic Institution (Ewing, Vine, & Worzel 1946; Ewing, Wollard, Vine & Worzel 1946).

Sand, either fine or coarse, appears according to these sources to cover the major portion of Georges Bank; occasionally it is mixed with broken shells, mud, or pebbles. Stony bottom also occurs. Ripple marks on the mud or sand, indicating the effect of bottom currents, appear in the photographs and such invertebrates as sand dollars, hermit crabs, star fish, and sea clams are also seen in many of the pictures.

Types of invertebrates taken by the dredge on Georges Bank (Smith & Harger 1874) were: Crustacea; Annelida; Mollusca; Echinodermata. There were approximately 30 to 40 species of each. Several of the crustacean species taken by the dredge were also caught by the stramin net in the present investigation. The decapod, *Dichelopandulus leptocerus*, was taken many times in the dredge by Smith & Harger and was reported as "common"; in the stramin net it was caught occasionally and had a relative numerical abundance of 0.3% per standard haul for all cruises. Of the amphipods caught by the dredge, there were twelve species also found in the stramin collection. Only two of these, *Pontogenia inermis* and *Unciola irroruta*, were taken at more than 50 out of a total of 296 stramin hauls, however; and of these two, only *Pontogenia inermis* occurred many times, having a relative numerical abundance of 1.5% per standard haul for all stations. The most abun-

dant Crustacea taken by the stramin net, such as *Themisto compressa, Monoculodes edwardsi, Neomysis americana, Thysanoessa inermis,* or *Crago septemspinosus,* were not taken in the dredge by the 1874 expedition.

VOLUMETRIC ABUNDANCE OF THE PLANKTON

The volumetric abundance of all the plankton taken in the stramin net was estimated on the basis of amount caught per standard haul for each station. The average volume per standard haul for each cruise was then calculated. These data were divided into average volumes for day hauls (6 a.m. to 6 p.m.) and night hauls in order to determine whether any differences in volume occurred due to various diurnal changes in the activity of the plankton which might affect the catches.

TABLE 2. Comparison of total plankton volumes caught by stramin net. Average volumes per standard haul for total plankton at all stations in each cruise and comparison of average volumes for day and night hauls.

CRUISE	Date	AVERAGE VOLUME IN CC.		
		Total	Day	Night
89....	September 1939	53	51	62
93....	January 1940	66	51	75
95....	March 1940	35	43	26
96....	April 1940	75	82	66
97....	May 1940	132	86	184
98....	June 1, 1940	188	166	216
100....	June 11, 1940	141	160	126
112....	March 1941	63	36	83
113....	April 1941	42	44	39
114....	May 1941	54	46	64
116....	June 1, 1941	214	251	190

An examination of Table 2 shows that for the plankton as a whole individuals are caught by the stramin net with approximate equal efficiency during both night and day. In only two cruises was either the night haul greater than the day haul, or vice versa, by more than two fold. For May, 1940, there were four unusually large night tows that consisted chiefly of sagittae. If these values, which range from 246 cc. to 634 cc., are omitted from the calculations, the average of 113 cc. results, which is less than twice the day haul of 86 cc. For March, 1941, if two unusually large night hauls of 438 cc. and 250 cc. due to an abundance of *Neomysis americana* are omitted, the average night value is reduced to 50 cc., which is less than twice the average day value of 36 cc. Thus the plankton as a whole does not show a marked tendency to escape the net by seeing and avoiding it any more easily during day than at night.

The vertical movements of some individual species in the plankton will be discussed in a subsequent section of this paper, but an examination of Tables 3 and 4 show that for the plankton as a whole there is no marked vertical migration during day or night. This condition, although contrary to what might be expected, probably indicates that while individual species may migrate vertically, the extent of their migration is either relatively small or that the movements of the various species cancel each other. Turbulence may also tend to confuse the pattern of diurnal movement. Data from April and June, 1940 were used in the tables because of the number of night and day hauls and the variety of organisms in the plankton sampler catches during those cruises.

The question may be raised that the plankton sampler or stramin net failed to catch organisms that remained very close to or rested on the bottom during the day. Examination of the plankton sampler catches, in addition to those given in Tables 3 and 4, showed that amphipods were more consistently caught at Second-depth or Deep levels by day than were euphausiids. Hence, it is unlikely that unsampled schools of euphausiids were present, for although the active euphausiids might be supposed to avoid easily the small mouth of the plankton sampler, good agreement with stramin net catches was obtained on many occasions when euphausiids were present. Clarke, Pierce, & Bumpus (1943) also demonstrated that the catch of the plankton sampler for active animals can be relied upon.

Table 2 illustrates the gradually increasing and decreasing monthly variations in the average volumes of plankton that corresponded to each cruise. In 1940, minimum and maximum average values of 35 cc. and 188 cc. per standard haul were found in March and June 1 respectively; or, assuming that an average of 300 m.^{3} of water was filtered during the

TABLE 3. Comparison of the vertical distribution of the more numerous species in plankton sampler hauls. The average number per cubic meter when present and the average percentage of the total number of organisms taken at each level at stations in Cruise 96, April, 1940, for day and night hauls is presented. Species which occurred at one station only in the day and night hauls are omitted. The number of stations at which each species was caught is given in parenthesis in the first two columns.

STATIONS AT WHICH THE SECOND DEPTH HAUL EXTENDED TO THE BOTTOM.

Organisms	No. OF STATIONS		AVERAGE NO. /m^3 WHEN PRESENT		AVERAGE PERCENTAGE AT EACH LEVEL		
	Day	Night	Day	Night		Day %	Night %
Monoculodes edwardsi.....	6(4)	9(9)	1.2	0.9	Shallow	0	23
					2nd Depth	100	77
Neomysis americana.....	6(1)	9(2)	0.6	0.2	Shallow	0	61
					2nd Depth	100	39
Thysanoessa inermis.....	6(1)	9(4)	0.2	0.7	Shallow	100	66
					2nd Depth	0	

STATIONS AT WHICH THE SECOND DEPTH HAUL DID NOT EXTEND TO THE BOTTOM.

Themisto compressa.....	7(3)	3(1)	0.3	0.4	Shallow	52	100
					2nd Depth	48	0
					Deep	0	0
Monoculodes edwardsi.....	7(2)	3(1)	1.2	0.9	Shallow	48	0
					2nd Depth	0	78
					Deep	52	22
Thysanoessa inermis.....	7(4)	3(2)	0.1	0.2	Shallow	0	40
					2nd Depth	13	60
					Deep	87	0

TABLE 4. Comparison of the vertical distribution of the more numerous species in plankton sampler hauls. The average number per cubic meter when present and taken at each level at stations in Cruise 100. June 11, 1940, for day and night hauls is presented. Species which occurred at one station only in the day and night hauls are omitted. The number of stations at which each species was caught is given in parenthesis in the first two columns.

Organisms	No. Of Stations		Average No. /m³ When Present		Average Percentage At Each Level		
	Day	Night	Day	Night		Day %	Night %
Stations At Which The Second Depth Haul Extended To The Bottom.							
Monoculodes edwardsi	12(3)	4(4)	5.0	0.5	Shallow	0	8
					2nd Depth	0	92
Neomysis americana	12(4)	4(1)	43.3	0.2	Shallow	48	10
					2nd Depth	52	100
Stations At Which The Second Depth Haul Did Not Extend To The Bottom.							
Themisto compressa	10(6)	10(3)	0.2	0.1	Shallow	40	80
					2nd Depth	21	13
					Deep	39	7
Monoculodes edwardsi	10(0)	10(6)	0	0.5	Shallow	0	16
					2nd Depth	0	33
					Deep	0	51
Meganyctiphanes norvegica	10(0)	10(3)	0	0.3	Shallow	0	50
					2nd Depth	0	48
					Deep	0	2
Thysanoessa inermis	10(6)	10(2)	1.0	0.8	Shallow	0	0
					2nd Depth	18	50
					Deep	82	50

standard haul (for discussion of standard haul, see page 235) the range is from a March minimum of 0.1 cc./m.³ to a June maximum of 0.6 cc./m.³ The same general rise also occurred in 1941 except that in this year the low point came in April, a month later than in 1940. In both years, there was approximately a five-fold difference between the greatest and least average monthly volumes.

The maximum individual catches were also considered. If all volumes of more than 300 cc. per standard haul or approximately 1 cc./m.³ were selected from the data, no cases were found for September, 1939, nor for January and March, 1940. One case occurs in April, three in May and five each June 1 and June 11. Of these, the highest value does not exceed 1200 cc. per standard haul, or approximately 4 cc./m.³ During 1941, there was one case in March, none in April or May and nine cases in the June 1 Cruise. The 1941 results closely resembled those found in the preceding year. It is important to note that the maximum average volumes and the maximum individual volumes both occurred in June.

An estimate of the plankton production on Georges Bank can also be judged from a comparison made between stramin net average volumes and the average volumes taken by the plankton samplers at the same station. The plankton sampler data was obtained from another part of the Georges Bank investigation.

The stramin net had a #00 silk inner tail and thus caught some of the smaller organisms; the fine meshed #2 silk nets of the plankton sampler caught both large and small organisms. Thus, the catches to some extent include the same fauna. From Table 5, it is seen that the volumes of the plankton sampler are usually greater than those of the stramin net volumes, the variation being less during the January-March period when there were presumably smaller numbers of the smallest plankton available, and largest during the June period when maximum numbers of the smallest plankton might occur. This, no doubt, is because that bulk of the smaller organisms which the stramin net fails to catch, is greater in volume than that bulk of the larger plankton caught by the stramin net. With these reservations in mind, examination of Table 5 indicates the approximate richness of the plankton on Georges Bank. Sampler average volumes range from 0.2 cc./m.³ to 1.7 cc./m.³; stramin average volumes from 0.2 cc./m.³ to 0.7 cc./m.³

TABLE 5. Comparing the average volumes from plankton sampler and stramin net. Average volumes calculated in cubic centimeters per cubic meter taken by plankton sampler and stramin net when both were towed at the same station.

Cruise	Plankton Sampler cc. /m³	Stramin Net cc. /m³
93 January 1940	0.22	0.22
95 March 1940	0.48	0.11
96 April 1940	0.99	0.25
97 May 1940	1.13	0.44
98 June 1, 1940	1.21	0.62
100 June 11, 1940	1.23	0.47
112 March 1941	0.22	0.21
113 April 1941	1.16	0.14
114 May 1941	1.16	0.18
116 June 1, 1941	1.78	0.71

Again realizing that the stramin net fails to retain some of the smaller organisms, a rough comparison (Table 6) can also be made with data given by Bigelow & Sears (1939) which summarizes the more extensive measurements of plankton volumes along the east coast of North America and North European waters.

Bigelow & Sears regard the most representative maximum single hauls of plankton yet recorded from American waters to be: 6.9 cc./m.³ taken in the offing of New Jersey; 2.0 cc./m.³ taken in the Gulf of St.

TABLE 6. Volumes of plankton along the east coast of North America, Northern Europe and Georges Bank.

Locality	Estimated cc./m³
Cape Cod to Chesapeake Bay	0.4 - 0.8
Gulf of Maine	0.05- 0.7
Nova Scotia Shelf	0.3 - 0.4
Iceland to Ireland	0.2 - 0.8
Norwegian Sea to North Sea	0.3 - 0.6
Present investigation of Georges Bank:	
Stramin Net	0.2 - 0.7
Plankton Sampler	0.2 - 1.7

Lawrence; and 1.0 cc./m.^{3} from the Scotia Shelf and from West Greenland. In the light of these statements it is reasonable to conclude that Georges Bank supports a rich plankton.

SPECIES COMPOSITION OF THE PLANKTON

In the collection of Plankton made by the 1.5 meter stramin net, a total of 57 species of larger Crustacea were identified. These species are listed below.

DECAPODA
Crago septemspinosus (Say)
Dichelopandulus leptocerus (Smith)
Spirontocaris liljeborgii (Danielssen)
MYSIDACEA
Erythrops erythrophthalma Goës
Neomysis americana (Smith)
EUPHAUSIACEA
Euphausia krohnii Brandt
Meganyctiphanes norvegica (M. Sars)
Nematoscelis megalops G. O. Sars
Thysanoessa inermis (Krøyer)
AMPHIPODA
Annonyx nugax (Phipps)
Acanthonotosoma serratum (O. Fabricius)
Autonoe websteri (G. O. Sars)
Apherusa tridentata (Bruzelius)
Ampelisca spiñipes Boeck
Ampelisca macrocephala Lilljeborg
Argissa typica Boeck
Byblis gaimardii (Krøyer)
Bathyporeia norvegica G. O. Sars
Calliopius laeviusculus (Krøyer)
Ericthonius brasilensis (Dana)
Eusirus cuspidatus (Krøyer)
Rhachotropis inflata G. O. Sars
Stegocephalus inflatus Krøyer
Syrrhoe crenulata Goës
Tiron acanthurus Lilljeborg
Tmetonyx noblis (Stimpson)
Eusirus propinquus G. O. Sars
Hoplonyx cicada (O. Fabricius)
Hyperia galba (Montagu)
Halirages fulvocintus (M. Sars)
Hyperoche kroeyeri Bovallius
Haloops tubicola Lilljeborg
Hippomedon serratus (Holmes)
Hippomedon propinquus G. O. Sars
Hippomedon denticulatus (Bate)
Leptocheirus pilosus Zaddach
Menigratus obtusifrons (Boeck)
Melphidippa goesi Stebbing
Melphidippa spinosa (Goës)
Melita dentata (Krøyer)
Monoculodes edwardsi Holmes
Paradaliscidae sp.
Probomedeia fasciata Krøyer
Pontoporeiidae sp.
Photis reinhardi Krøyer
Pleustes panoplus (Krøyer)
Parathemisto oblíva (Krøyer)
Pontogenia inermis (Krøyer)
Phoxocephalus holboli (Krøyer)
Rhachotropis oculata (Hansen)
Tmetonyx quadratus Kunkel
Themisto compressa Goës f. *compressa* Goës
Thyposa minuta Boeck
Unicola irrorata Say
Vibilia armata Bovall

SELECTION OF PREDOMINATING SPECIES

The ecological importance of the larger Crustacea can be judged in two ways: by frequency of occurrence—being caught at many stations over a wide area; or by relative abundance at any station. An organism that swarmed in great numbers at few stations might be just as important as one which occurred sparsely at many. To simplify selection of predominating species among these larger Crustacea, it was decided to choose arbitrarily the criteria of 50 hauls in order to establish a frequency of occurrence (Table 7). On this basis of the ten frequently occurring Crustacea, Monoculodes and Thysanoessa, were caught in more than 50% of all hauls.

TABLE 7. Frequency of occurrence of the crustacean species. Species of Crustacea which occurred in more than 50 out of total of 332 stramin net hauls and the number of hauls in which they occurred.

SPECIES	*No. of Hauls*
Monoculodes edwardsi	182
Thysanoessa inermis	171
Decapod larvae	133
Themisto compressa	101
Crago septemspinosus	98
Schizopoda immature[1]	91
Neomysis americana	89
Meganyctiphanes norvegica	72
Dichelopandulus leptocerus	67
Pontogenia inermis	64

[1] The immature mysids and euphausiid larvae were grouped together as Schizopoda immature.

If the relative abundance of the crustacea is now considered, as in Table 8, in which the species more abundant than 200 and 500 per standard haul are shown, nine of the most frequently occurring (Table 7) again appear. The species are marked by an asterisk in Table 8. These Crustacea are therefore both widely distributed over Georges Bank and also occur in significant numbers.

TABLE 8. Abundance of the crustacean species. Cases in which each species were more abundant than the indicated numbers.

	NUMBER OF STANDARD HAULS.	
	More than 200 Specimens	*More than 500 Specimens*
SPECIES		
**Monoculodes edwardsi*	55	17
*Schizopoda immature	36	18
*Decapod larvae	35	12
**Neomysis americana*	23	15
**Crago septemspinosus*	7	1
Euphausia krohnii	6	1
**Themisto compressa*	5	0
**Thysanoessa inermis*	4	2
**Meganyctiphanes norvegica*	4	1
**Pontogenia inermis*	3	2
Nematoscelis megalops	3	0
Erythrops erythropthalma	1	0

Seasonal changes in the catches of the larger Crustacea is set forth in Table 9, which presents for each cruise the average number per stramin haul of the more abundant types and plainly illustrates both the relative plentifulness and widespread distribution of such species as Monoculodes, Thysanoessa, Neomysis, and Crago.

TABLE 9. Average number per standard haul per cruise of the species most abundant in Table 7. Numerals in parentheses represent the number of hauls at which organisms were caught during each cruise.

CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
DATE	Sept. 1939	Jan. 1940	Mar. 1940	Apr. 1940	May 1940	Jun. 1, 1940	Jun. 11, 1940	Mar. 1941	Apr. 1941	May 1941	Jun. 1, 1941
Total hauls made	36	13	28	26	30	36	36	33	34	28	32
Species											
Monoculodes edwardsi	120(15)	319(11)	45(14)	254(22)	218(22)	41(19)	79(12)	63(16)	64(14)	32(20)	59(21)
Pontogenia inermis	9(7)	85(4)	0.6(4)	5(9)	0.4(4)	1(5)	3(2)	1(6)	2(9)	33(8)	1(6)
Themisto compressa	71(31)	87(12)	0.3(2)	0(0)	1(7)	1(10)	1(8)	0.5(7)	.07(3)	2(10)	7(10)
Neomysis americana	75(5)	250(6)	0.3(4)	306(10)	39(10)	1(2)	1(3)	581(14)	125(12)	251(13)	31(9)
Thysanoessa inermis	47(15)	26(8)	13(20)	14(21)	13(20)	0.2(3)	1(5)	62(29)	8(15)	12(25)	1(7)
Meganyctiphanes norvegica	89(23)	1(2)	4(7)	6(6)	4(4)	3(4)	7(4)	6(7)	9(4)	16(5)	9(6)
Euphausia krohnii	91(11)	28(4)	0.5(2)	5(2)	4(2)	3(2)	7(3)	0(0)	.07(1)	0.2(1)	11(3)
Schizopoda immature	0(0)	2(2)	0(0)	1(1)	19(2)	134(20)	169(32)	1(1)	0(0)	14(7)	998(29)
Decapod larvae	141(23)	1(1)	123(2)	10(3)	73(10)	85(15)	63(24)	7(5)	59(18)	115(23)	684(5)
Crago septemspinosus	59(9)	71(6)	1(7)	11(15)	30(13)	2(6)	1(7)	14(13)	5(7)	3(8)	8(7)

Certain species have been mentioned as occurring frequently but only in small numbers, others have reversed this trend. If the organism with a low relative abundance is a large crustacean, and thus important in the food cycle, this fact must be weighed when the ecological importance of the species is considered. For instance, Dichelopandulus, found among the ten most frequently occurring species has a fairly wide distribution on the bank, but the largest single catch of it was 172 per standard haul. Usually it occurred in small numbers and averaged one per standard haul per cruise. Presumably this species keeps rather close to the bottom and only small numbers normally come within range of the net or the prawns may escape capture by actively swimming. Because of its size and its wide distribution, however, we include Dichelopandulus among the ten predominating species in the collection.

The three organisms listed in Table 8 but not found among the most frequently occurring species; namely, Euphausia, Nematoscelis, and Erythrops which occurred in 31, 47, and 34 hauls respectively, are examples of organisms which do not have a widespread distribution on Georges Bank but are occasionally caught in moderately large numbers there. Erythrops is almost invariably taken on the south edge of the bank between the 100 m. and 200 m. contours. Nematoscelis and Euphausia are usually found beyond the 200 m. contour on the slopes of the bank, not always, however at the same station. Since these organisms are more typically slope than bank types, they were not numbered in the list of predominating species.

To conclude, therefore, it can be said that with exception of Dichelopandulus, the ten most frequently occurring species are also found in greatest relative abundance on the bank. Such species as Euphausia, Nematoscelis, and Erythrops, which sometimes are caught in abundance, were not taken more frequently because they were not typically bank inhabitants and were only caught when stations were made at the edge of the bank near the 200 m. contour. Only a few such stations were made on each cruise. There was no other species which occurred in numbers more limited than 200 per standard haul, or in less than 50 hauls the size of which might make it especially important in the food cycle of Georges Bank. Therefore, the evidence presented by the preceding data suggests that the following crustaceans are the predominating species in the stramin net collection.

Monoculodes edwardsi
Themisto compressa
Pontogenia inermis
Neomysis americana
Thysanoessa inermis
Meganyctiphanes norvegica
Crago septemspinosus
Dichelopandulus leptocerus
Schizopoda immature
Decapod larvae

The distribution of these species on Georges Bank will be discussed in the following section.

CONSIDERATION OF PREDOMINANT SPECIES

MONOCULODES EDWARDSI

OCCURRENCES

Monoculodes edwardsi comprises an average of 40% of the amphipods taken at all stations, and thus is pre-eminently the most abundant species of this

group. It is odd that this amphipod, apparently so numerous on Georges Bank, had never previously been reported from this region. Individuals had been taken in New England waters for it was first described as a new species from Woods Hole by S. J. Holmes in 1903. Shoemaker (1930) reports that 500 specimens were taken by dredge and young fish trawl at eight stations in the Gulf of St. Lawrence and the Magdalen Islands at depths varying from 10 m. to 75 m., the deepest at which it had previously been reported. In the present collection, specimens were caught at depths from 40 m. to 120 m. This amphipod has not yet been noted outside the northeast coast of North America. Dr. Shoemaker kindly examined some of the amphipods of the present collection and confirmed the identity of *Monoculodes edwardsi*.

The eleven cruises to Georges Bank made by the *Atlantis* obviously extended over a comparatively short period. Additional data over a longer span of years concerning the occurrence of Monoculodes might reveal that it periodically fluctuated in abundance on the bank, which would perhaps account for the failure of previous expeditions to capture this now abundant amphipod.

Inspection of the distribution chart Figure 3, shows that Monoculodes may have a widespread disposition inside the 100 m. contour of Georges Bank throughout most of the year. During eleven cruises, it was taken in deeper water only in the following cases: beyond the 100 m. line, ten hauls chiefly with catches less than ten per standard haul; beyond the 200 m. line, three hauls with all catches less than five per standard haul. The amphipod was taken on or beyond the 100 m. line more frequently on the north edge of the bank than on the south edge.

The distribution pattern for Monoculodes was the same in both 1940 and 1941, but the average catches (Table 9) were smaller in the latter year, being 54 per standard haul per station per year.

Although Monoculodes may be found over most of the bank throughout the year, it is completely absent from a large portion of the shallow central bank during June, as a scrutiny of the charts for June 1940 and 1941 (Fig. 3) will show. With the approach of summer, the amphipod appears to be restricted to a relatively narrow belt along the 100 m. contour of the south edge of the bank. Presumably, its occurrence is favored by cooler water now found between the warmest bank water covering the central regions and the warm Atlantic water of the south slope. Prevailing bottom temperatures (Fig. 2) might suggest this view. Wide differences in numbers per standard haul between stations practically adjacent characterize the distribution of Monoculodes during spring and early summer. These differences, easily seen for June 1940 and June 1941 in Figure 3, might indicate that the organism is here actively avoiding unfavorable environmental conditions. However, a distribution based on low temperatures fails to explain the widespread occurrence of Monoculodes in September when the bank water is relatively warm (Fig. 2). It is possible, as Edwards & Irving (1943) have shown for certain Crustacea, that this amphipod has the ability to become adjusted to seasonal changes in temperature, and during spring, avoids water to which it later becomes adjusted.

To account for distribution of the species solely on the basis of variations in water temperatures oversimplifies the question, however, and neglects such factors as: influence of water movement, centers of reproduction, accessibility of food, or the nature of the bottom. The possible effect of some of these factors can, unfortunately, only be surmised in the absence of direct evidence. Inspection of Figure 3 shows that the homogeneous water of the Mixed Area, indicated by a heavy broken line on each chart, does not limit the distribution of Monoculodes. Substantial catches are commonly made both inside and outside the Mixed Area. Occurrence of Monoculodes is thus less closely circumscribed by water of the Mixed Area than was the pelagic chaetognath *Sagitta elegans* investigated by Clarke, Pierce, & Bumpus (1943). This widespread horizontal distribution of Monoculodes, coupled with the length of time it flourishes on the bank during the year, suggests that reduction in numbers and decrease in distribution during spring may as probably be related to death of adults after breeding as to a reaction to unfavorable ecological factors in the environment, since the organism appears to be indigenous to Georges Bank and not a temporary resident.

Largest single catches of Monoculodes were made in January, April, May, June and September in 1940 and during April and June in 1941. Thus, there does not seem to be a marked seasonal maximum. The peak catches were made at stations where the bottom temperatures varied from 11° C. to 3° C. If the catches of more than 500 per standard haul are considered the data can be arranged as in Table 10.

TABLE 10. Cruises having catches of more than 500 per standard haul.

Cruise	No. of Hauls	Bottom T°
89 Sept. 1939	2	11° C.
93 Jan. 1940	4	5° C.
95 March 1940	–	
96 April 1940	3	3° C.
97 May 1940	4	5° C.
98 June 1, 1940	–	
100 June 11, 1940	2	6° C.
112 March 1941	–	
113 April 1941	1	4° C.
114 May 1941	–	
116 June 1941	1	5° C.

Of the 17 catches having more than 500 per standard haul, 15 were made in the southwest or south central region of the bank between the 50 m. and 100 m. contours; hence this area may be considered the region of maximum abundance. Concentrations usually dwindle rapidly beyond the 100 m. line at the margin of the bank.

Vertical distribution of Monoculodes (Tables 3 and 4), indicates that in general there were fewer organisms in the shallow stratum than in the second

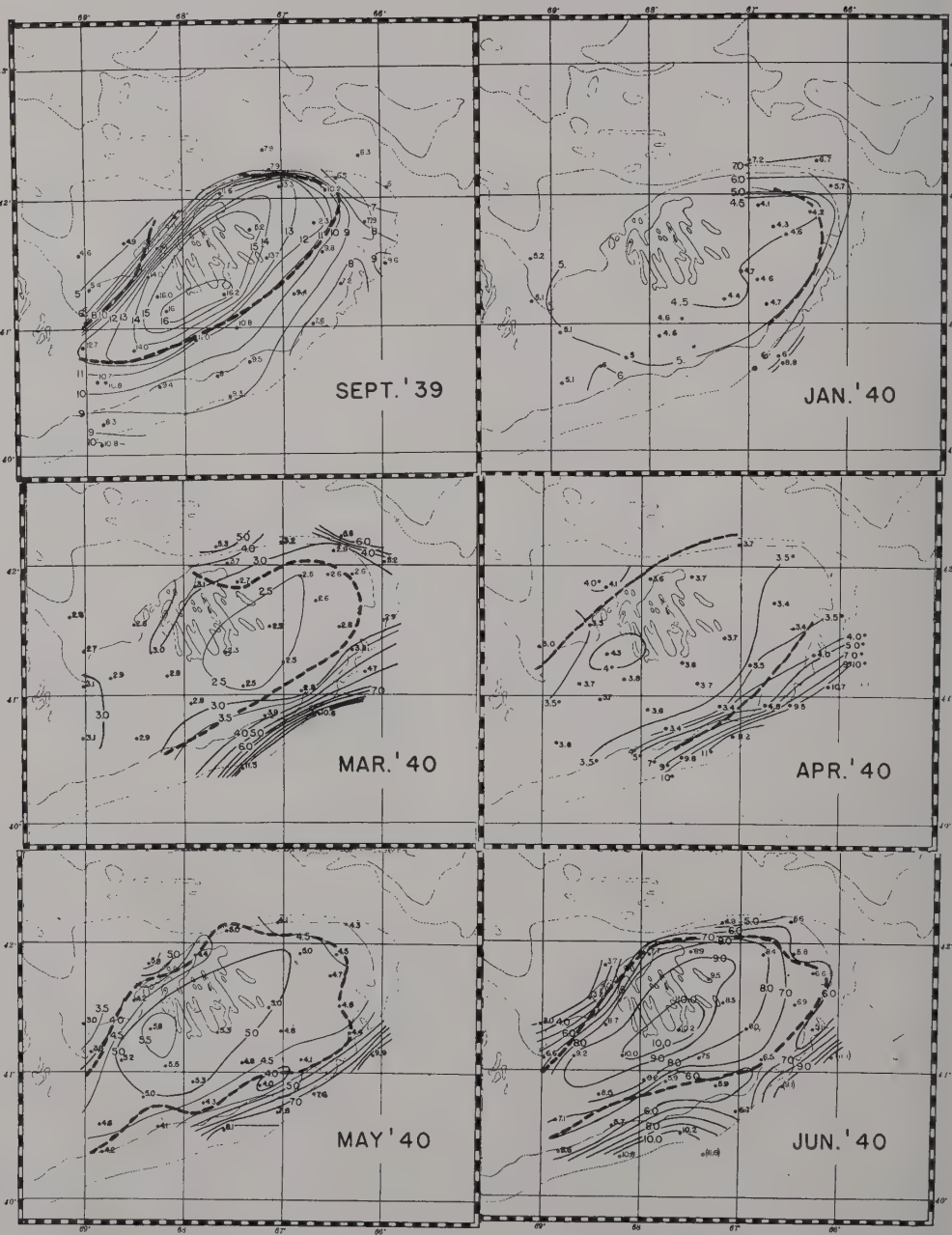

FIG. 2. Temperatures in degrees centigrade at the bottom of Georges Bank during September 1939, January, March, April, May and June 1940. Boundary of Mixed Area shown by heavy broken line.

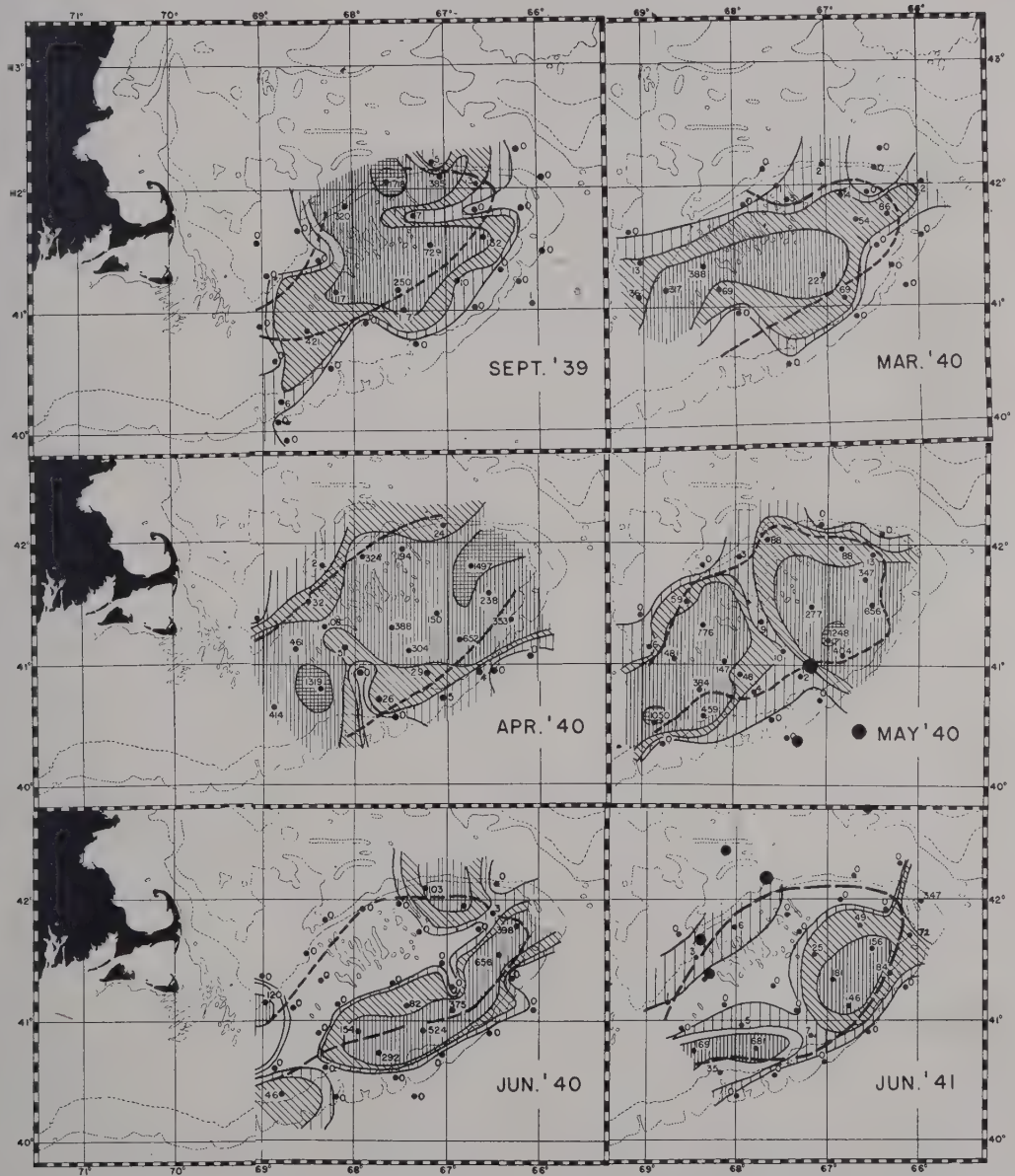

FIG. 3. Distribution of *Monoculodes edwardsi* on Georges Bank for September 1939, March, April, May and June 1940, and June 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line. Contour lines representing concentrations of 1, 10, 100, 1000, have been drawn on all distribution charts. Progressively dense cross-hatching indicates areas of increasing numerical abundance.

depth of deep stratum. There was some tendency to move upward at night, but even at night there were more individuals caught at the deeper levels. In other cruises, not given in the tables, Monoculodes was rare in the shallow stratum.

BREEDING AND GROWTH

Comparatively little is known about the life history of amphipods. Holmes (1901) states, "aquatic amphipods are negatively phototropic,—fertilization takes place immediately after the female moults." Smallwood (1905) could determine no age groups for *Orchestra palustris,* a terrestrial amphipod, owing to wide variations in length. Eggs required 12 days to hatch in July. Skutch (1926) studied the tube build-

ing amphipod of Maine tidal pools, *Amphito rubricata*, and reports that breeding occurred from July until late August, egg bearing females, and females with young were taken throughout this period. Dunbar (1945) states that *Themisto libellula*, important as the chief food for harbour seals in the coastal waters of Baffin Land, is positively phototrophic, can grow as much as 2 mm. per month, has a breeding period during spring and probably a second in autumn so that two generations exist simultaneously.

Concerning the habits of planktonic amphipods in the open ocean, even less is known. On Georges Bank in the northeast section during September, 12 Monoclodes, 3-4 mm. in length were caught. In January, 16 specimens 3-7 mm. in length were caught, on the southwest section. Large numbers of adults were caught in these areas at the same time. During May and June, both the Plankton sampler and stramin net caught many female Monoculodes carrying eggs in brood pouch. With the exception of the young stages caught in September and January, no marked variation in size was noticeable among Monoculodes population. Individuals were measured from time to time to check their lengths against the adult size of 9 mm. given by Shoemaker. Very little variation from this length was found in the collections.

The occurrence of egg-bearing females in June and young stages in September and January indicate that the reproduction period on Georges Bank probably takes place during summer. Adult Monoculodes can be caught throughout the year on Georges Bank.

Fish (1925) examined the plankton of the Woods Hole region by daily tows throughout the year and recorded the appearance and disappearance of individual members of the fauna. Fish states that "*Monoculodes edwardsi* breeds from November to January." This conclusion was reached because Monoculodes, which he considered benthonic, appeared in the plankton tows at that time and not because egg-bearing females or larvae were found in the tows. On Georges Bank Monoculodes was not completely benthonic, it was sometimes pelagic and the bank breeding period previously mentioned as probably lasting through summer covers a different interval than the breeding period at Woods Hole. The appearance of Monoculodes at Woods Hole in November, however, may have been related to the sudden change in the temperature of the well-stirred Woods Hole waters which averaged, as data in Fish's report show, 20° C. from June to September. During October the temperature began to fall and in November dropped suddenly from about 13° C. to 4° C. When Monoculodes was appearing in the plankton at Woods Hole, from November until it disappeared in January, the temperatures ranged from 10° C. to 0° C. Distribution of this amphipod on Georges Bank shows that while the crustacean was sometimes caught in areas having bottom temperatures as high as 16° C., it was usually found in colder water. Hence one may speculate that the occurrence of Monoculodes in the Woods Hole plankton is associated with the November temperature change and therefore may not be solely due to a breeding migration.

THEMISTO COMPRESSA

OCCURRENCES

Two representatives of *Themisto*, the forms *compressa* and *bispinosa*, have long been known to abound off the northeast coast of the United States, typically on the coastal banks. These two "formae" are, however, now considered as one species (Stephensen 1924) and in this paper they are treated as *Themisto compressa*.

Bigelow (1926) states "Themisto is one of the most characteristic, if not abundant, members of the plankton of the offshore waters of the Gulf of Maine where it was taken at approximately 90 per cent of the stations outside the 100 meter contour during July and August."

In the present investigation (Fig. 4) Themisto was widely dispersed over Georges Bank in September. At 10 stations there were catches of more than 100 per standard haul. In January fewer stations were made and the entire bank was not sampled but catches during January suggest that no marked change in distribution had occurred since September. Average number of individuals caught per standard haul in January was somewhat less than during the fall cruise, although in the southwest area there were three rich tows, one being 426 per standard haul, which exceeded the highest individual catch of September. Distribution in both 1940 and 1941 was very similar; the May and June 1941 catches were slightly larger than in the previous year.

From March to May, Themisto is practically absent from the major portion of the bank. Individuals begin to reoccur during May and June along the north and south margins (Fig. 4). Hauls of Themisto were made both inside and outside the Mixed Area. Catches outside the Mixed Area are usually larger even in September when the organism is widely distributed over the bank.

These facts suggest that Themisto always present in the Gulf and offshore (Bigelow & Sears 1939) is borne to the bank either by water movement or by the animal's own power of locomotion. If water movement alone was involved Themisto would probably not be so conspicuously absent from the bank during winter and spring. At least some of the animals swept on and off the bank would be caught. Therefore, it would seem that in spite of water movement the organism is able by its own efforts to avoid being carried to the bank. The reason for its nonoccurrence during winter may thus indicate lack of favorable environmental condition for growth or breeding.

One may judge from the distribution of Themisto during September and January that maximum occurrence of the organism is associated with comparatively high temperatures (6° C. to 14° C.) on Georges Bank. Average number per standard haul per cruise indicated a fall maximum and a midwinter minimum (Table 8). Bigelow (1926) found a somewhat similar incidence in the Gulf of Maine.

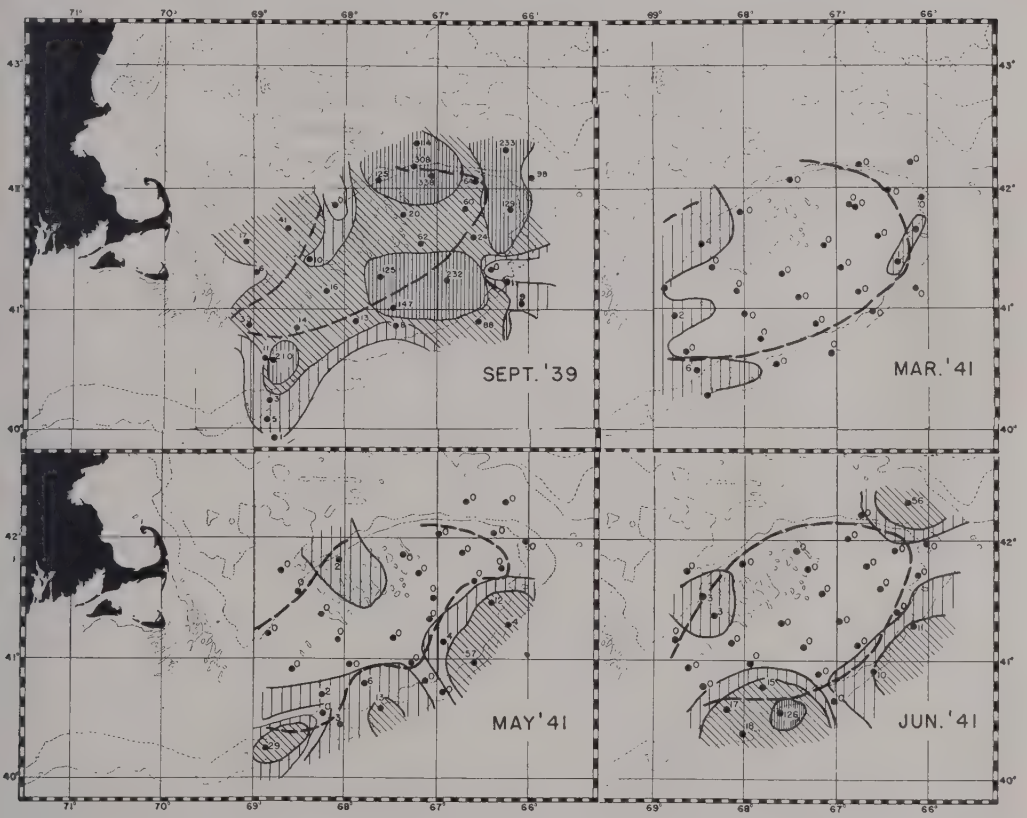

FIG. 4. Distribution of *Themisto compressa* on Georges Bank for September 1939, March, May, and June 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

A summer and early autumn maximum contrasted with an early spring minimum. Bigelow also states that Themisto, while abundant in the Gulf, is rarely caught off Nova Scotia. The cold waters of that area may form an unfavorable environment for it.

Distribution of Themisto on Georges Bank suggests, therefore, that both water movement and suitable environmental conditions, of which temperature is an important factor, are associated with its maximum occurrence. Extremes of temperature, above 15° C. and below 5° C., are apparently unfavorable for it. The animal's minimum occurrence is apparently due to its ability to avoid these conditions.

The vertical distribution of Themisto (Tables 3, 4) indicates that rarely was it caught on shoal areas of the bank where the second-depth stratum extends to bottom. Wherever deeper hauls were made, however, largest catches occurred principally in the shallow stratum and next in the second-depth stratum. Even by day, the organisms were more abundant in the shallow stratum, but at night this tendency was accentuated. This distribution in the upper water layers may be related to the partiality of Themisto for relatively high temperatures as previously mentioned.

BREEDING AND GROWTH

Young specimens appeared in the tows during January 1940, and June 1941, but numbers were comparatively few and no length frequencies were recorded. Breeding may possibly take place during summer when no cruises were made. Bigelow (1926) found young stages in the Gulf of Maine during every month from February to October, and adults with eggs at two stations on the western section of Georges Bank in July. Fish & Johnson (1937) state that rich tows of breeding Themisto were made on the northeast section of Georges Bank in September 1932. It may be assumed, therefore, that on Georges Bank breeding of Themisto takes place during summer.

PONTOGENIA INERMIS

OCCURRENCES

At one station on Georges Bank, Smith & Harger (1874) took a single specimen of Pontogenia in their dredge. Rathburn (1905) reports that Pontogenia occurs from polar seas to Vineyard Sound, is very

common in the Gulf of St. Lawrence and is taken on all kinds of bottom at Mt. Desert Island from shore to 400 m. Shoemaker (1930) states that Pontogenia is very common on the coast of New England, but of much rarer occurrence on the coast of Europe. At Woods Hole (Fish 1925), it occurred from mid July to mid August, a much shorter time than did most of the other species recorded.

In the present investigation on Georges Bank for all but two cases, both with catches one per standard haul, Pontogenia was taken within the 50 m. contour by the stramin net. In 80% of the cruises, it was mainly caught on the southwest section of the Bank. Tows of more than 100 per standard haul were made chiefly in the southwest section as follows: 1 haul, September 1939; 3 hauls, January 1940; 1 haul, June 11, 1940; 2 hauls, May 1941. Hauls of more than 500 per standard haul were made twice, once each in June 1940, and in May 1941, both in the southwest section. Very few specimens were caught during March and May 1940, for in each of these cruises there was a total of five catches only with no catch having more than eight per standard haul. Average number of specimens per standard haul per cruise indicates a mid-winter minimum; a fall and spring maximum (Table 8).

Pontogenia occurs in greatest abundance on the southwest section of the bank, but numbers in contiguous areas may vary within wide limits, viz: from a maximum of 937 per standard haul to 0 per standard haul at adjacent stations.

Pontogenia, seldom taken by the plankton samplers, was always caught in the second-depth stratum whenever it did occur during day or night tows.

The present investigation produced no data concerning the breeding and growth of Pontogenia. Adults measured an average of 12 mm., which is similar to the lengths given by Sars and Shoemaker.

NEOMYSIS AMERICANA

OCCURRENCES

Although Neomysis was not reported in the plankton from Georges Bank or the Gulf of Maine by Bigelow, it has been found in large numbers in the plankton of the Bay of Fundy during April (Fish & Johnson 1937). South of Cape Cod (Bigelow & Sears 1939), it extends to Chesapeake Bay and is confined to the inshore belt of the Continental Shelf to a distance of 30 miles from land, where it persisted in approximately the same volume from February to July. In Chesapeake Bay, it was found most plentiful in December and January. At Woods Hole, Fish (1925) states that it is present from December to April, and Smith (1879) found young and adults in Vineyard Sound during April and May. Hence, north or south of Cape Cod it generally is caught in greatest abundance during winter and spring. Perhaps Neomysis was absent from Georges Bank, as noticed by Bigelow, because the plankton collection from there was largely a summer one.

In the present collection from Georges Bank, the capture of Neomysis showed that it was very rarely caught beyond the 100 m. margin of the bank, and its distribution, with four exceptions, was always within the limits of the Mixed Area (Fig. 5). Of the four cases taken outside the Mixed Area, all had less than six individuals per standard haul. Maximum abundance invariably occurred on the shallow central axis of the bank, in the southwest, center, or northeast regions with a gradual decrease in numbers towards the margins. Throughout the year, the abundance of Neomysis fluctuated from a late fall (September to January) maximum to a winter low in February or March. Large numbers again occurred during spring but subsequently decreased in June (Fig. 5). In March 1941, catches were high in contrast with those of the previous March. Larger hauls than in the preceding year were also made during April and May 1941, although June again brought reduced catches. These results may perhaps be related either to difference in physical conditions that favor the occurrence of Neomysis or to biological differences, such as a variation in the number of animals breeding, or to a combination of these factors. Moreover, no hauls were made in certain areas of the central bank during March 1940, which may also account for some of the differences observed. Indicative of variation in physical conditions may be the circumstance that during 1941 water temperatures slightly higher than the previous year's prevailed on the bank during winter (Table 1). This eddy of even slightly warmer water may have resisted dislocation by gales or by currents from the Gulf of Maine. The Mixed Area itself is somewhat more extensive in March 1941 than in March 1940. Such physical conditions may have favored the concentration of Neomysis on the central bank in the spring of 1941 (Fig. 5). The distribution of the mycidacean suggests that catches are reduced during the coldest interval of the year and a second minimum may also occur during summer, the warmest interval.

It is interesting to observe that Neomysis sometimes occurs in very large swarms on the bank. There is also greater contrast between high and low catches than in any other species studied. When the averages per standard haul are compared (Table 8), it must be kept in mind that in September 1939, or March 1941, for example, the high averages are due to one or two of these large hauls (Fig. 5).

The swarms, which usually occur on the long axis of the bank, may be found at only one or at several stations during the same cruise, either in the southwest, center or northeast regions. They are probably related to the breeding of Neomysis which will be discussed presently.

Vertical distribution of Neomysis (Tables 3, 4) shows that it is usually taken in those areas of the bank where the second-depth stratum reaches to bottom, that is, within the 75 m. contour. This illustrates good agreement between catches of the plankton sampler and the stramin net, for the net caught very few outside the 100 m. contour. No consistent vertical migration, however, is displayed. The animal's vertical movements, apparently erratic, are not

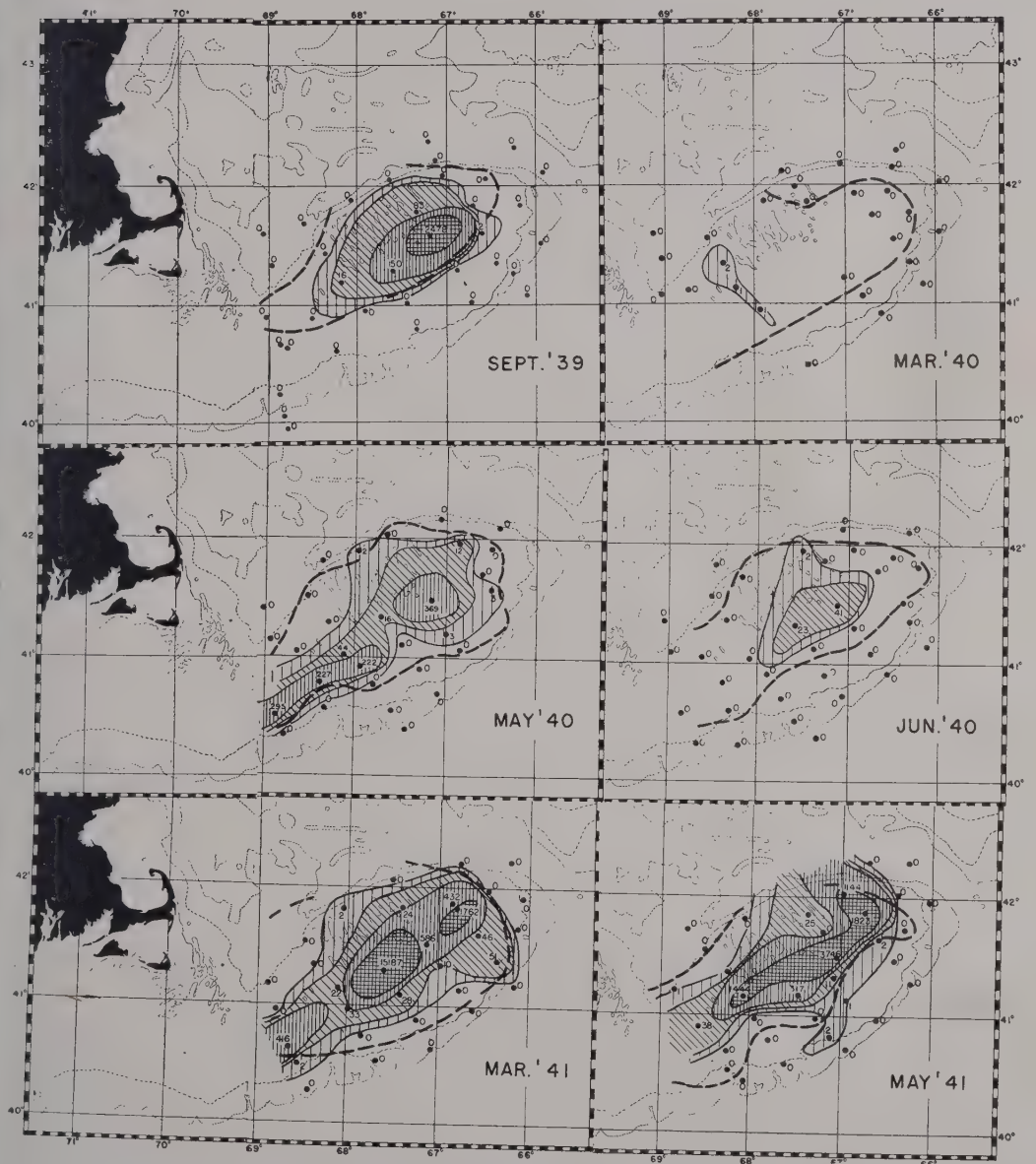

FIG. 5. Distribution of *Neomysis americana* on Georges Bank for September 1939, March, May, June, 1940; March and May 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

subject to general conclusion. During daylight, greater numbers seem to be caught near bottom.

BREEDING AND GROWTH

Smith (1879) states that the breeding of Neomysis took place during spring in Long Island Sound and Casco Bay, Maine, since young and adults were taken together there during spring and summer. Smith also caught young and adults in Vineyard Sound during April and May. For *Mysis stenolepis*, a related species, Smith reports females with eggs in December in Long Island Sound and females with either empty egg sacs or carrying fully developed young in April and May.

Average length of Neomysis in the present collection was 13.4 mm. Approximately 200 individuals were measured during 1940 and little variation was

observed in adult length except that the largest individuals, up to 14-15 mm., were usually taken in May. It is perhaps regrettable that more measurements were not made either in 1940 or in 1941, but the uniformity of the catches did not then invite closer investigation of lengths. Smith (1879) gives a range of 10-12 mm. for adults in Long Island Sound, where they were commonly found in the stomachs, of shad, mackerel, herring and flounder during May.

In the Georges Bank plankton, no egg-bearing female Neomysis were observed, but in June numbers of immature mysids were caught. At least one possible breeding period is shown by the distribution data (Fig. 5). During March 1941, a large catch, 15,187 per standard haul, was made at one station. As the major portion of the catch was adults, the animals were probably swarming to breed. It is true that March 1940 (Fig. 5) does not show any similar breeding group, but on this cruise the central area was not sampled by the stramin net on account of stormy weather. Perhaps this failure to test thoroughly the bank's population may explain the marked contrast between the March results. In both years hauls of more than 1,000 per standard haul were made during the April and May cruises, and there was also a general increase in distribution on the bank as though the animals were spreading out from larger concentration centers. As this increase is a logical development in 1941, following the large March concentration, it may be assumed that a similar concentration occurred in March or early April 1940, though there is no direct evidence of it.

The data indicate, therefore, that there is probably a spring breeding period for Neomysis which in the main agrees with the findings of Smith for the New England coast.

THYSANOESSA INERMIS

OCCURRENCES

Due to its circum-polar distribution, its relatively large size (17 mm.) and the considerable numbers in which it frequently occurs, Thysanoessa plays an important role in the planktonic community of Northern seas. Euphausiid abundance in the Gulf of Maine has been noted by many investigators during the past century. Smith (1879) states that from April to October in the cold waters of Eastport, Maine, Thysanoessa and *Meganyctiphanes norvegica*, swarming on the surface "for miles," were preyed upon by schools of mackerel, pollock and immense flocks of gulls. Bigelow (1926) reported that Thysanoessa occurred more regularly over the Gulf of Maine than any other euphausiid. It was taken at 50% of the stations throughout the offshore areas though never in large numbers, but during March and April was not found on Georges Bank. Except at Eastport, it was not taken at all in the coastal zone during summer.

South of Cape Cod, Thysanoessa extends to Chesapeake Bay (Bigelow & Sears 1939) but it occurs there much less frequently than in the Gulf of Maine and always more than 30 miles from land. Smith (1879) found it abundant in Vineyard Sound during January.

In the present investigation of the plankton of Georges Bank, Thysanoessa was found to have a somewhat general distribution over the central and northern portions of the bank within the 100 m. contour during fall and winter and to disappear during summer (Fig. 6). Numbers occurring at all times were relatively small (Table 9).

Inspection of Figure 6 shows that Thysanoessa in March 1940 had only two catches of more than 50 per standard haul, these were made on the northern edge of the bank where the majority of individuals were caught in March. Few catches were made at this time on the south portion of the bank. During April 1940, there was little change in distribution, but in May even fewer catches were made in the southern and central regions, although individuals were still taken all along the north edge of the bank. In June, there was an abrupt decrease in the occurrence of adult Thysanoessa over the entire bank and catches were made only on the northern slopes beyond the 100 m. contour. Tows in September, however, showed Thysanoessa well distributed inside and outside the Mixed Area, although fewer were taken in the southern region than elsewhere. Not only in September, but also in other months the organisms seemed to occur at comparatively isolated centers of abundance on the northeast, central and northwest portions of Georges Bank (Fig. 6). For all months except September, the numbers of Thysanoessa in Figure 6 refers to adults only, as there were practically no immature stages in the other tows. Some larval stages of Thysanoessa were caught during September, however, and these were included in the September data. Stages previous to calytopis, although undoubtedly present, were not identified.

During 1941, the distribution pattern was a repetition of the previous year. Greater numbers of individuals occurred in March, however, when five tows having more than 100 per standard haul were made.

These data indicate, therefore, that while Thysanoessa does not occur in large numbers on Georges Bank, as only four tows having more than 200 per standard haul were made during all cruises, this euphausiid nevertheless has a somewhat general distribution on central and northern portions of Georges Bank from September to May.

A scrutiny of bottom temperatures (Fig. 2) shows that while Thysanoessa tends to occur in waters below 10° C., catches can be made when the bottom temperature varies from 2° C. to 16° C. Hence the occurrence of Thysanoessa undoubtedly depends on a combination of environmental factors in which temperature may be of secondary importance. The euphausiid probably tends to avoid extremes of temperature. For example, in the offshore waters of the Gulf of Maine, it is very likely present throughout the year, although it is distributed more widely during summer than in winter, indicating that sections are then unfavorable. However, it is never

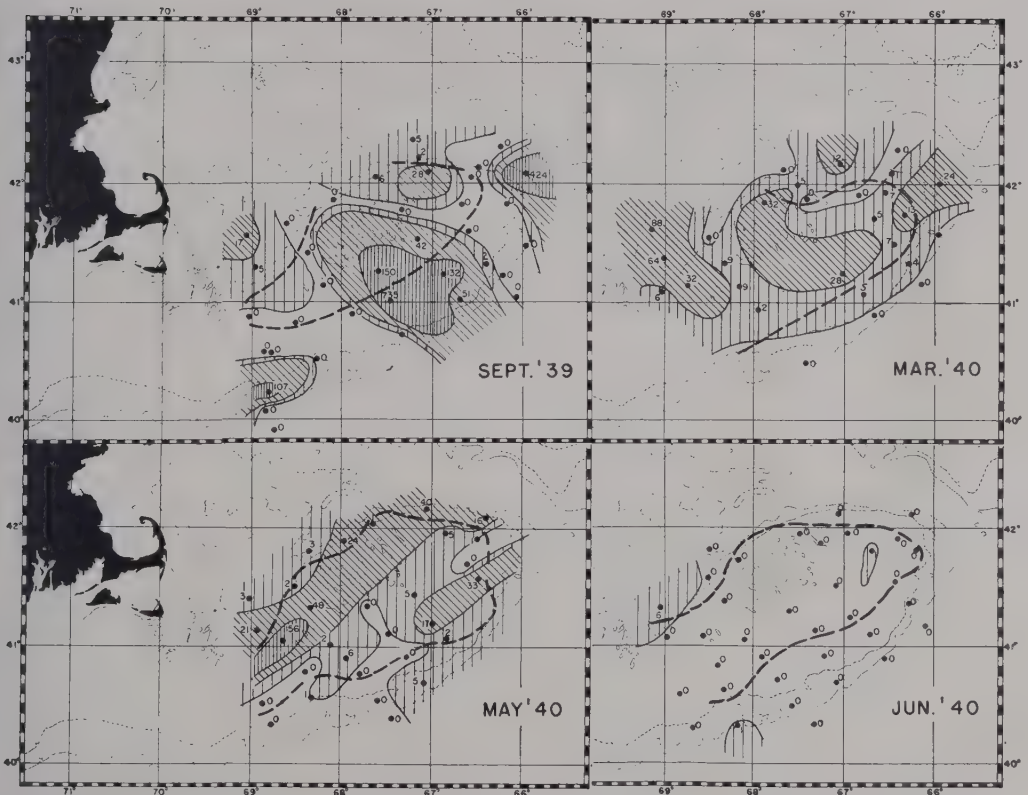

FIG. 6. Distribution of *Thysanoessa inermis* on Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

common in the coastal regions of the Gulf of Maine except within the Bay of Fundy, and it is rarely found as far seaward as the continental edge.

Bigelow (1926) considers the most notable seasonal fluctuation shown by Thysanoessa was its absence from Georges Bank in March and April. In the present investigation, no reduction in numbers was noticed during March or April in either 1940 or 1941, but each year there was a definite disappearance of adults during June. The animals may have died after breeding or migrated from the bank to avoid an unfavorable physical environment, but since water temperatures in June are generally lower than they are in September when Thysanoessa occurs on the bank, stimulus to migrate is evidently not one solely concerned with water temperature. If the animals lack ability to make extensive horizontal migrations, their presence or absence on the bank will be chiefly influenced by prevailing currents. Possible effect of these currents on the distribution of the Crustacea will be analyzed in a subsequent discussion.

Regarding the vertical distribution of Thysanoessa, Fish & Johnson (1937) found that catches in the Bay of Fundy were largest at night. Other observers agree that this organism has never been found in abundance at the surface in any part of the Gulf of Maine except at Eastport. Usually largest catches have been made in nets working at 40-80 meters depth. In the present investigation, at stations with depths less than 75 meters, more individuals were taken in the shallow stratum than at the second-depth level. Tows in depths greater than 75 meters found the animals in the second-depth or in the deep stratum. There was some tendency for Thysanoessa to rise to the surface at night, although at depths less than 75 meters, individuals were caught in the shallow stratum equally well during day or night. Tables 3 and 4 illustrate this vertical distribution of Thysanoessa.

BREEDING AND GROWTH

Within the Bay of Fundy, Fish & Johnson (1937) found Thysanoessa breeding during March and April (eggs and nauplii) and the May tows showed a 300% increase in the number of juvenile stages of euphausiids (Thysanoessa and Meganyctiphanes) as compared with previous months. There appeared to be for Thysanoessa in this area only one breeding period ending in late June. Fish & Johnson also considered that Thysanoessa passed the win-

ter in post larval stages and matured with rising temperatures in the following spring. Bigelow (1926) reported young (unidentified) euphausiids abundant during August in the Gulf of Maine.

In the present investigation, eight egg-bearing females were caught in the March 1940 tows on the northeast part of the bank. Large numbers of euphausiid larvae were found in June. Undoubtedly these young stages are chiefly juvenile Thysanoessa as a subsequent discussion of them and of the breeding habits of the other euphausiid, *Meganyctiphanes norvegica,* will indicate. The appearence of these larvae may explain, perhaps, the abrupt decrease in the number of adult Thysanoessa at the beginning of summer (Fig. 6). The probability of a single annual brood of Thysanoessa in the Gulf of Maine has already been mentioned. Hence the following life cycle may occur on Georges Bank: adults breed during spring and with the onset of summer either the major portion die after breeding or are dispersed by changes in the physical environment. Adults, at any rate, disappear from the catches and Thysanoessa on Georges Bank is now represented only by the juveniles which occur abundantly in the summer tows.

Thysanoessa at various stages of growth were measured in 1939 and in 1940. In the September 1939 cruise most of the individuals in the collection appeared to be immature (Table 11). There was a gradual increase in average length from September 1939 to May 1940 as the brood reached maturity. In June 1940, evidence of what may be a new brood appears in the length-frequencies. Average length of 17.0 mm. in May indicates that a majority of the adults are mature. The length of mature Thysanoessa has been given as 17-19 mm. (Hansen 1915, Lebour 1926).

TABLE 11. Length frequency distribution of *Thysanoessa inermis* 1939-1940.

Date	Length in mm.																				Average
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
September 1939	..	5	1	9	2	7	7	4	5	..	..	..	..	..	..	..	..	..	..		13.3
January 1940	..	..	..	10	..	1	4	18	28	3	4	1	..	..	..	..	..	..	..		14.0
March 1940	3	..	..	24	3	14	10	30	134	45	87	21	8	12	..	1	..	..	1		15.3
April 1940	..	..	..	5	..	5	..	..	17	2	16	15	..	16	..	1	..	..	..		16.6
May 1940	..	..	..	..	..	..	..	..	14	18	39	52	6	69	..	..	..	..	..		17.1
June 1940	3	4	1	..	..	2	..	..	4	..	9	..	1	8	..	1	..	..	..		16.9

At all events the data indicates that breeding of Thysanoessa on Georges Bank may take place during spring. It is assumed that the larvae develop during summer and winter and mature during the following spring when water temperatures rise.

MEGANYCTIPHANES NORVEGICA

OCCURRENCES

Meganyctiphanes, the largest euphausiid in our plankton collection and one of the most numerous and economically important euphausiids of northern seas, on both sides of the Atlantic, has been regularly found throughout the year by many investigators in the deeper waters of the Gulf of Maine. It usually occurs outside the 100 m. contour, within the central basin of the Gulf of Maine, but depth of water by itself is apparently no bar to its distribution as it has been taken in shoal areas (Bigelow 1926, Fish & Johnson 1937). Bigelow states "it does not swarm in great numbers in the Gulf except in the northeast part where hauls indicated as many as 275 per square meter of sea surface." On Georges Bank, however, Meganyctiphanes was only taken twice by Bigelow, a fact which he is at lost to explain as there was nothing in the physical state of the water there to account for its absence.

In the present investigation of Georges Bank, Meganyctiphanes was taken inside the 100 m. contour of the bank in winter and spring on four occasions only. That is to say, during the eleven cruises, Meganyctiphanes was almost completely absent from the major portion of the bank in these seasons. However, the euphausiid was then regularly caught outside the 100 m. contour and in deeper water beyond the 200 m. contour, on both north and south edges.

Inspection of Figure 7 will show the distribution of Meganyctiphanes for several winter and spring cruises. The catches were consistently larger on the northern side of the bank where the spring maximum of 280 per standard haul was made. For both years, however, during spring only nine hauls exceeded 100 per standard haul, showing that Meganyctiphanes does not at this season have the numerical strength of such forms as *Monoculodes edwardsi* or *Neomysis americana.*

The results of the September 1939 cruise, however, show a completely different picture. Meganyctiphanes was then widely distributed both inside and outside the Mixed Area. Although nine catches of more than 100 per standard haul were made, i.e., as many as in all the other cruises added together, the large swarms were nevertheless rather scattered about the bank. Largest catches again were made beyond the 100 m. contour; the maximum was as high as 1175 per standard haul at a station just beyond the 200 m. contour off the northeast tip. Average numbers per standard haul per cruise (Table 8) show little seasonal fluctuation except for September.

Hence, it seems obvious that under certain conditions Meganyctiphanes can occur in moderate abundance on Georges Bank. It is odd that Bigelow found no Meganyctiphanes in the September plankton from this region. September 1939 chart (Fig. 7) shows, however, that on the northeast end of the bank, where the *Grampus's* stations were made, Meganyctiphanes was least plentiful inside the 100 m. line. If this condition is characteristic of the region, the *Grampus* could possibly have missed finding them there.

Distribution of Meganyctiphanes just described may suggest that the low temperatures on the bank during winter are unfavorable for the occurrence of

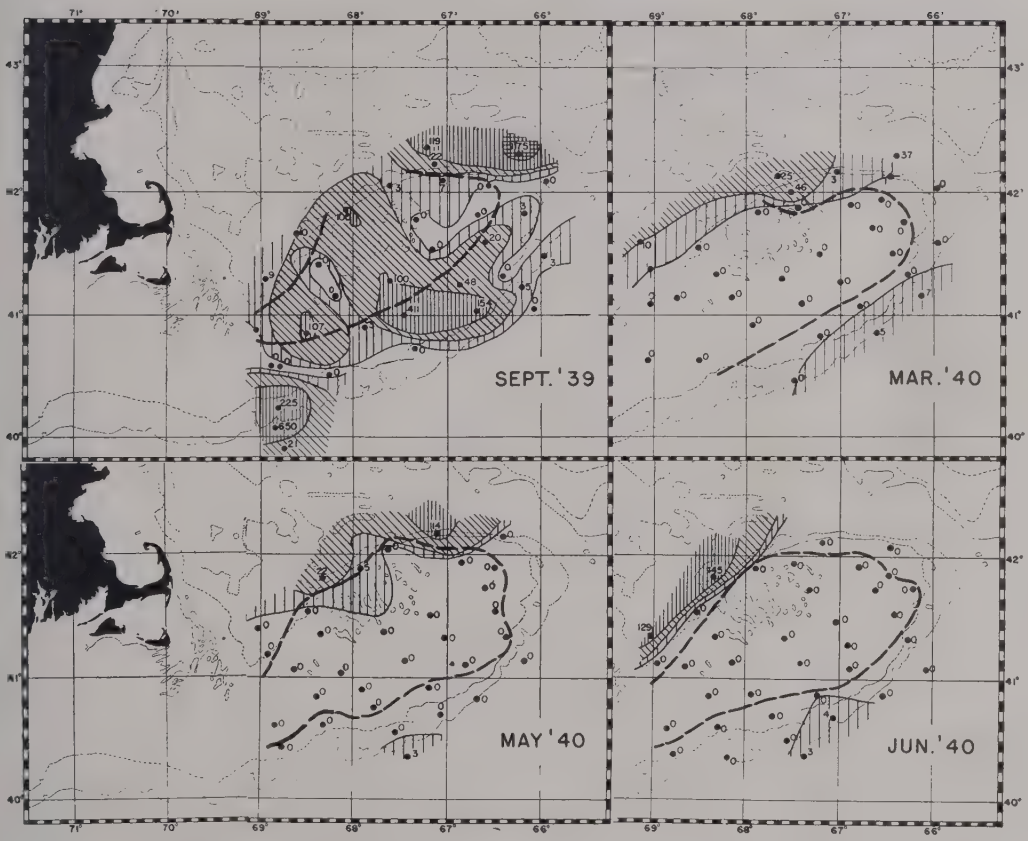

FIG. 7. Distribution of *Meganyctiphanes norvegica* on Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

this euphausiid; but if comparison is made between the bottom temperatures on the bank (Fig. 2) and the distribution of Meganyctiphanes (Fig. 7), the organism was at times caught when the temperatures ranged from 3° C. to 16° C. If a specific cruise is selected, for example, March, 1940, which shows the coldest average temperature of the year, Meganyctiphanes was caught at stations with bottom temperatures from 3° C. to 11° C. During the April and the May cruises when the organism was caught in cool 5° water on the north side of the bank and warm (11°) water on the south side, the main portion itself had temperatures between those extremes, but in spite of these apparently suitable conditions no Meganyctiphanes were found there.

Observers have also noted that Meganyctiphanes tolerated a wide range of salinity, from 29-34 per mille, so that the slight seasonal changes on Georges Bank from 32-33 per mille would have no limiting effect on its occurrence.

It would appear, therefore, as Bigelow suggested, that other factors in addition to the physical state of the water must govern the distribution of Meganyctiphanes on Georges Bank. The most important of these factors is undoubtedly currents, the effect of which will be subsequently discussed.

As previously mentioned for *Thysanoessa inermis*, with which it frequently occurs, Maganyctiphanes is not usually caught on the surface in the Gulf of Maine except at Eastport and other parts of the Bay of Fundy. All observers agree that the normal habitat of Meganyctiphanes is in the moderate temperature and reduced light of the deeper strata, but it may as Bigelow (1926) states, "rise to the surface at any time either by the action of active vertical currents or in pursuit of food."

The vertical distribution of Meganyctiphanes in the recent cruises to Georges Bank shows that it can be caught at night equally well in both shallow and second depth strata (Table 4). In June 1940, however, on the cruise selected for the investigation of vertical distribution, Meganyctiphanes was caught only at night, even at stations beyond the 100 m. and 200 m. contours where organisms would be most likely to occur; thus the animals successfully avoided the sampler during day or else were very close to

bottom and escaped on that account. However, records not included in Table 4 show that when caught in daylight, Meganyctiphanes was usually at deep or second-depth levels. Thus there appears to be a tendency for Meganyctiphanes to rise into the shallow stratum during the night; although Bigelow (1926) considered that its appearance at the actual surface was independent of the time of day.

BREEDING AND GROWTH

In the waters of the English Channel to which it comes to breed from the deeper parts of adjoining seas, Lebour (1926) found female Meganyctiphanes with eggs and also eggs in cleavage stages in the plankton during late winter and spring.

Fish & Johnson (1937) reported eggs and larvae of Meganyctiphanes abundant in the tows at different parts of the Bay of Fundy from May to August. Meganyctiphanes usually began breeding in the spring a few weeks later than *Thysanoessa inermis* but Meganyctiphanes also had an August spawning at that time. This breeding was less extensive than during spring. Fish & Johnson also considered that at least a part of the Meganyctiphanes population of the Bay of Fundy probably survived a second year, as there were adults 35 mm. in length in November when the younger adults were not yet 24 mm.

No attempt has yet been made in the present investigation to study eggs other than those of fishes, nor has differentiation of the euphausiid larvae been attempted; but a preliminary study of the June 1940 tows failed to show conspicuous number of Meganyctiphanes larvae in them. Adult Meganyctiphanes were absent from the greater portion of the bank during spring but were invariably present along the margin. Distribution of euphausiid larvae (Fig. 9) indicates that considerable hatching had been in progress on or near the bank during May and June 1940. Conditions were similar in 1941. Hence we believe that while the larvae may be chiefly *Thysanoessa inermis*, the most numerous euphausiid on the bank during spring, young stages of Meganyctiphanes must also have contributed to the collection since adults are always present on the periphery of the bank. Little direct evidence, however, is available concerning the breeding of Meganyctiphanes on or near Georges Bank.

Length-frequency measurements were made of juveniles and adult Meganyctiphanes for some of the cruises, and the average lengths were as follows:

Cruise	*Minimum*	*Maximum*	*Average Length*
Sept. 1939	7	30	13.8 mm.
March 1940	10	35	24.1 mm.
April 1940	10	32	21.5 mm.
May 1940	10	35	24.9 mm.
June 1, 1940	10	35	24.3 mm.
June 11, 1940	15	35	25.5 mm.

The largest Meganyctiphanes caught by Hansen (1915) in deep water south of Georges Bank was 35 mm. Average length of adult Meganyctiphanes given by several authors is 25 mm. The brood of the same year thus appears to be present in the vicinity of Georges Bank from September to June. These Meganyctiphanes, as previously suggested, are not most likely to be the result of bank spawning, if indeed such breeding occurs at all, but have probably come from the Gulf of Maine or waters to the south of the bank. The occurrence of adults 30 mm. in length supports the view of Fish & Johnson that the old stock of Meganyctiphanes is not wholly replaced but survives a second year. Since there were few large adults of this size, however, the evidence is rather inconclusive.

It may be concluded that Meganyctiphanes is rarely found on the central Georges Bank area except during autumn when widely scattered centers of abundance occur. The bank appears to have little or no egg production itself. With the exception of the September catches, there is little evidence of young stages in the tows. Nevertheless, breeding of Meganyctiphanes must have taken place near the bank in the months preceding September in order to produce 13 mm. juveniles in that month. It is doubtful whether breeding takes place on the bank; hence the population must have been recruited from marginal areas. Consequently, Meganyctiphanes on the bank during September are probably migrants which will either be borne away by movements in the water mass during winter, or having increased in size and swimming ability they may become capable of retreating from unfavorable physical conditions. Bigelow (1926) considered Meganyctiphanes much less tolerant of cold water than *Thysanoessa inermis* and stated that the winter contraction of Meganyctiphanes into the deeper portions of the Gulf of Maine probably begins in October. Thus the seasonable distribution of Meganyctiphanes of Georges Bank may be partly a function of temperature, but other less obvious factors are also undoubtedly important.

CRAGO SEPTEMSPINOSUS

OCCURRENCES

Crago septemspinosus is commonly found on the North American Atlantic coast from eastern Florida to Baffin Bay and may occur from shallow water to 450 meters on all kinds of bottom. Verril & Smith (1873) found Crago to be an important item in the food of fish in Vineyard Sound. This decapod is usually collected by a bottom dredge but has been taken by tow net (Sumner, Osburn, and Cole 1911; Fish 1925). On Georges Bank, it was often reported by Smith & Harger (1874) and was usually a "common" or "abundant" species in their dredge. Egg-bearing females have been reported common in Vineyard Sound throughout summer, and young stages have been taken from April to December at Woods Hole (Fish 1925). Bigelow & Sears (1939) state that south of Cape Cod, Crago, while never abundant, was more often caught during February and April than during June and July, which suggests that it rises (or is swept upward) from the ocean floor in significant numbers most commonly during winter when turbulent movements of water are most active.

In the present investigation, Crago was distributed

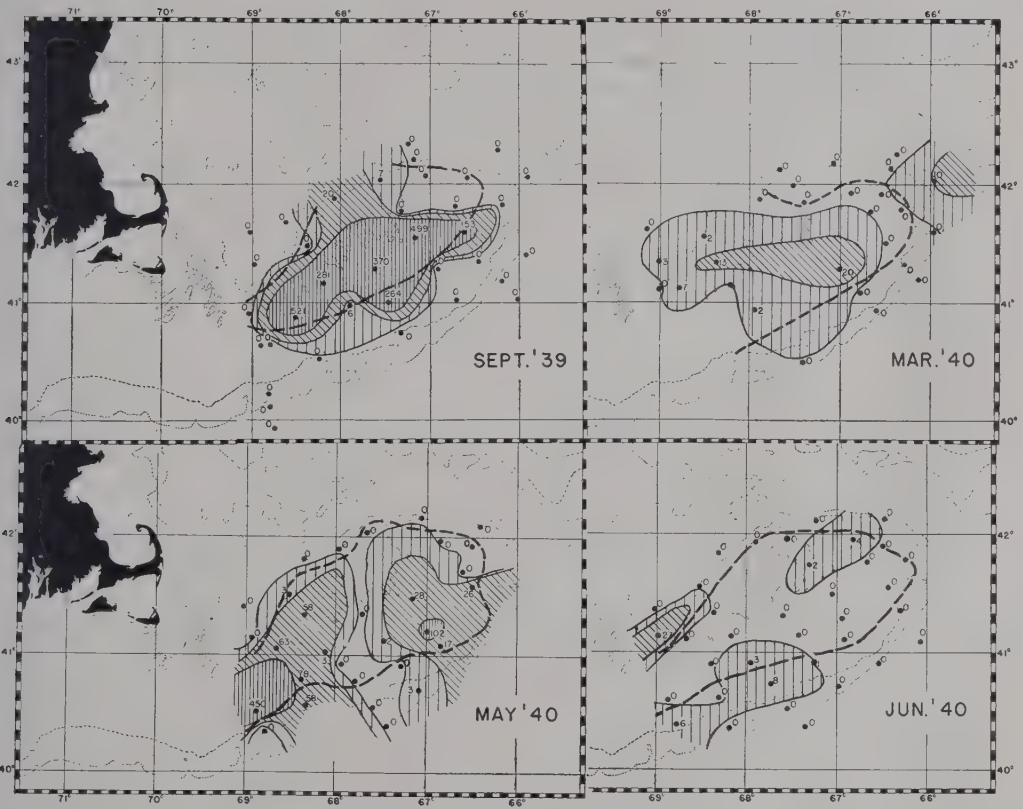

FIG. 8. Distribution of *Crago septemspinosus* of Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

over Georges Bank with a fair degree of regularity during all eleven cruises. Concentrations were richest during September and January, poorest in June (Fig. 8). Distribution in 1941 was similar, and in neither year is there any indication of the stock being recruited from the gulf or offshore. Catches were made both inside and outside the mixed area, but with few exceptions were always made inside the 100 m. contour of the bank, either because in deeper water the net did not reach near enough to bottom or the animals do not occur on the slope. With respect to numbers occurring in the tows, there were 2 hauls of more than 100 per standard haul in May, 6 in September and 3 in January. These aggregations may be associated with the breeding habits of the organism and will be discussed in a later paragraph.

Study of the vertical migration of Crago showed that although it was seldom caught by the plankton samplers, catches were more frequently made at the second-depth and deep stratum than in the shallow stratum. Time of day had no appreciable effect on the catches.

BREEDING AND GROWTH

The following averages were obtained from the measurements of individuals during several of the cruises:

Cruise	*Minimum*	*Maximum*	*Average Length*
89 Sept. 1939	5	20	11.4 mm.
93 Jan. 1940	7	27	17.0 mm.
96 April 1940	7	35	20.1 mm.
97 May 1940	10	30	20.1 mm.

References in the literature to length of Crago are rare. Rathburn (1882) states, "some adults from southern New England equal two inches in length (51 mm.) but the average length is much lower than this." Length of 60 mm. are, however, common for this decapod in Alaskan waters (M. J. Rathburn 1904).

Length-frequencies of Crago caught on the September 1939 cruise to Georges Bank show that these were chiefly immature individuals (Table 12). Needler (1941) found that the first post-larval or bottom stages measured about 40 mm. in length. It is presumed that Crago reaches maturity within a year,

TABLE 12. Length frequency distribution of *Crago septemspinosus* in millimeters, 1939-1940.

Month	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	35	Average
Sept.	1	7	31	20	10	36	9	16	8	7	13	3	8	2	2	2	...	...	...	...	...	...	...	...	...	...	...	11.4
Jan.	...	...	1	2	10	14	8	8	5	18	19	16	24	20	19	10	13	11	4	2	8	...	1	...	...	...	...	17.0
April	...	...	...	...	...	7	3	2	1	2	3	4	5	8	12	18	10	9	14	10	6	4	8	4	...	5	1	20.1
May	...	...	...	...	...	1	2	1	1	2	6	2	4	9	11	12	10	8	6	4	5	1	2	1	1	3	...	20.1

since egg-bearing females measuring 20 to 25 mm. in length commonly occurred in our early spring catches. Length-frequencies of individuals caught throughout the year on Georges Bank show no tendency to form even a bimodal pattern, although a life span of three years has been reported for some related groups, such as the Pacific Coast Pandalidae (Needler 1930). Separate groups of larger Crago representing older year-broods may congregate on the slopes of Georges Bank as do certain pandalids on the bank slopes of the Pacific Coast; such groups of Crago the stramin net may have failed to sample. During eleven cruises, however, our catches om Crago were invariably made inside the 100 m. contour. Obviously, in the present investigation, insufficient evidence permits no definite conclusions concerning the length of survival or maximum growth of Crago on Georges Bank, although data indicate a single annual brood which agrees with the findings of Fish & Johnson (1937).

Maximum numbers of juvenile Crago were taken in July at Woods Hole and during August in the Bay of Fundy where they were the most abundant benthonic larvae in the tows (Fish 1925, Fish & Johnson 1937). In the Gulf of St. Lawrence, breeding occurs from mid-June through July (Needler 1941).

The first egg-bearing females were observed in the Georges Bank tows during April 1940, others occurred in May and June. Many decapod larvae were caught in the May and June tows. These facts suggest that on Georges Bank, breeding of Crago probably begins during spring and continues into early summer. South of Cape Cod, Bigelow & Sears (1939) found in late June off New York that young stages of Crago occurred in mid-depth in such abundance as to be an important item in the general planktonic community. In the present investigation, the decapod larvae were not identified and will be discussed as a group later, but there is reason to believe that a large proportion of the decapod larvae found in the May and June tows on Georges Bank were juvenile Crago.

DICHELOPANDULUS LEPTOCERUS

OCCURRENCES

Dichelopandulus was the largest species of crustacean in our plankton collection from Georges Bank. This decapod has a wide distribution ranging along the northeast Atlantic Coast from eastern Long Island to Greenland. Less abundant south of Cape Cod than north of it, catches of Dichelopandulus in the Gulf of Maine have been reported where occasionally "more than a peck were caught in a single haul of the beam trawl" (Rathburn 1882). Presumably this was the result of one hour's tow. Rathburn states that Dichelopandulus associated with other species of shrimps, must have occurred in "immense shoals" in the Gulf of Maine as very large hauls were sometimes made, but on account of the activity of the animals such large catches were difficult to secure consistently. Dichelopandulus was reported "common" in several dredge hauls on Georges Bank by Smith & Harger (1874).

The distribution of Dichelopandulus on Georges Bank as determined by the present investigation showed that either the shrimp were scarce or the stramin net failed to catch them at the majority of stations. Catches were usually made on or near the 100 m. line and, with the exception of the South Channel region where some always occurred, were irregularly distributed from cruise to cruise along this contour. Only in September 1939 were any of these decapods caught on the central bank area. Greatest number of catches for any cruise was nine and the least four. The average catch per standard haul per cruise, based only on stations where the organism occurred, varied between 5 and 6 per standard haul, except for September 1939, when an average of 42 per standard haul was obtained. This higher average was chiefly the result of one haul, a catch of 172 per standard haul made on the central bank. Even if this catch is omitted, however, the resulting average of 23 per standard haul is still higher than the average of the other cruises. Hence greater numbers of Dichelopandulus appear to be on the bank in September. This abundance may be connected with the organism's reproductive cycle and will be discussed in a later paragraph.

Concerning the vertical distribution of Dichelopandulus little information is provided by the plankton sampler catches because this decapod rarely occured in them. Catches that were made were taken in the second-depth or deep stratum irrespective of time of day.

BREEDING AND GROWTH

During September the population of Dichelopandulus sampled by the stramin net was obviously composed of both juveniles and adults (Table 13). This September cruise is the only one which so clearly shows such a mixture of age-groups. The shrimp caught in succeeding months all appear to belong to one brood. The presence of large numbers of young as well as older individuals in September is probably responsible for the several large hauls in the month which, as previously mentioned, swelled the September average catch far above that of the other cruises.

TABLE 13. Length frequency distribution of *Dichelopandulus leptocerus* in millimeters 1939-1940.

Month	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	34	35	36	38	40	45	50	55	60	Average
September	5	1	12	10	4	20	3	19	4	4	3	..	4	4	2	4	1	..	2	..	6	1	1	1	..	1	..	1	2	1	1	19.3
March																8			1	..	4	..	2					1	1			30.5
April																6				2	12	..	3	6	..	..	3				3	34.8
May																											2	2	3	2	..	47.0
June 11																								1	..	1	3	1	7	2	..	46.5

Rathburn (1882) reported Dichelopandulus up to 100 mm. in length from Massachusetts Bay. No individuals of this size were taken during the present investigation, however, although egg-bearing females 55-60 mm. in length were caught during May and June 11, 1940. Rathburn stated that egg-bearing females (size not given) were caught during August and September in Massachusetts Bay. Hence, although little direct evidence of breeding was found, the presence of both egg-bearing females in May and June and numerous small immature specimens in September indicated that Dichelopandulus very probably breeds during summer on Georges Bank. Had cruises been made during summer perhaps additional evidence would have been obtained.

Concerning the life-cycle of Dichelopandulus little further is known. Length-frequency distribution (Table 13) does not suggest a series of year-groups, but insufficient individuals may have been measured to demonstrate adequately this possibility. The pandalidae of the British Columbia coast, such as *Panulus danae* and *Pandulus borealis* (adult length, 100-150 mm.) have been found to live for at least three years, and become mature in the autumn of the second year as males then reverse their sex to bear eggs in the third year (Needler 1930). The adults are only found in quantity beyond 100 meters although smaller specimens are found in the shoaler water.

Should Dichelopandulus have a life-cycle somewhat similar to these decapods the major portion of Georges Bank may be too shallow for the large adults. Most of the catches made on the bank were taken near the 100 meter contour, except those of the younger ones in September which occurred chiefly on the shallow central bank. As the animals increased in size they may have withdrawn from the main bank to the deeper slopes more favorable to adult life, and the stramin net would probably have failed to catch adults living close to bottom near the 200 meter contour. Nevertheless, the immature stages found in September may have been due partly to the breeding of such adults or they may have developed from larvae which had drifted on to the bank from the South Channel area or from Massachusetts Bay where large individuals have been caught in the past by Rathburn and others.

Although available data to support these conjectures is insufficient, the possibility is suggested that Dichelopandulus is the largest and longest-living crustacean in our collection from Georges Bank.

SCHIZOPODA IMMATURE

OCCURRENCES

When the tows were first examined and the organisms counted immature mysidae and euphausiid larvae were grouped together for, until the June cruises, very few occurred in the tows. Although mysids leave the marsupial pouch with a full complement of appendages and are in all important characters like the adult, whereas euphausiids go through a series of larval stages following their leaving the egg as a nauplius, the two groups were formerly classified as Schizopoda. In this present paper the immature mysidae and the euphausiid larvae have not been separated; they have for convenience been designated Schizopoda Immature, as the term although obsolete exactly describes in this particular case the organism under discussion. It may be noted, however, that the immature mysidae appeared less abundant than the euphausiid larvae.

Relatively few (one or two hauls per cruise) of the immature Schizopoda were taken by the stramin net from September to April. Hauls taken were made along the south or northeast edges of the bank, either near the 100 meter contour or in the deeper water beyond the 200 meter line. No hauls were made on the north edge or on the central bank during this autumn and winter period. With the approach of spring and extending into summer there was a distinct change in occurrence (Fig. 9). Catches per standard haul increased considerably during May 1940. In May, 1941 the increase was even greater and the distribution more widespread. During June in both years large numbers of individuals were caught all along the south margin of the bank and were also found in the west and north areas inside the 100 meter contour. In June, 1940 there were 15 catches of more than 100 per standard haul and one of more than 1000 per standard haul. Even greater numbers occurred during June 1941 when there were 20 catches of more than 100 per standard haul and 10 of more than 1000 per standard haul. In other respects the distribution of immature Schizopoda in 1941 followed the previous year closely. Hence the abundance of these organisms is, as far as our records show, minimal during autumn and winter; greatest during early summer.

In May, when the first marked increase in immature Schizopoda occurred, organisms were caught in greatest numbers beyond the 200 m. line on the south edge of the bank. They were entirely absent from the central bank until late June. Therefore, it would

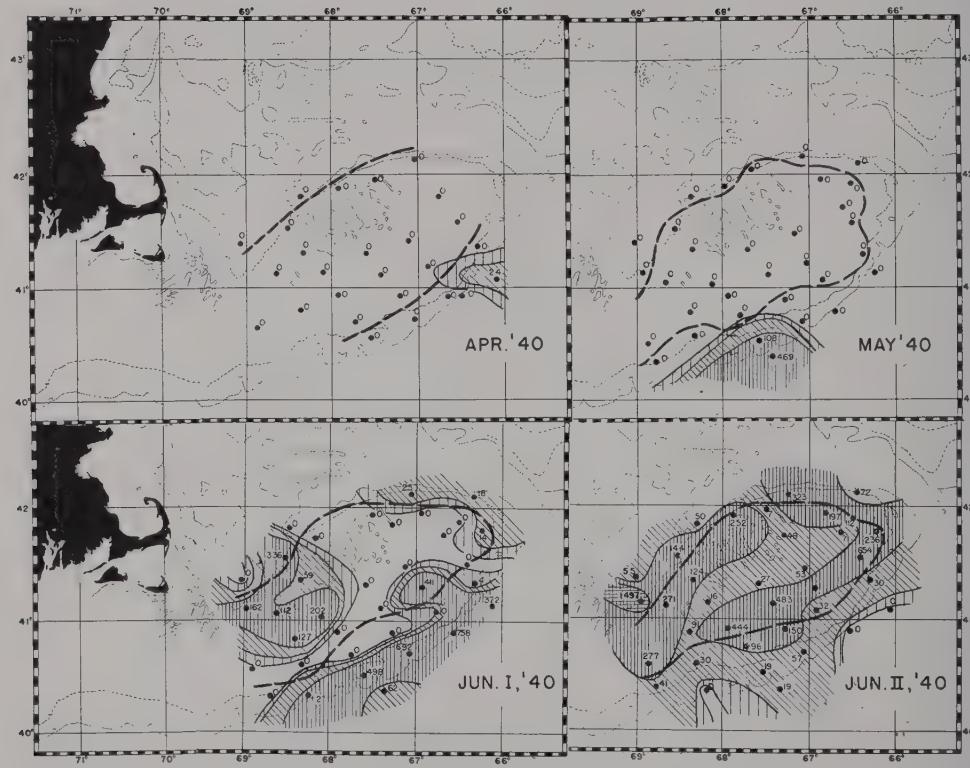

FIG. 9. Distribution of immature Schizopoda on Georges Bank for April, May and both early and late June cruises in 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

appear that adults contributing, for example, to the May and June collections, were breeding in deep water beyond the 200 m. margin of the bank. The distribution and breeding of *Neomysis americana* have already been discussed. From March to May, Neomysis occurred on the central regions always inside the 100 m. contour. Numbers decreased in June; increased again in September (Fig. 5). Obviously Neomysis did not contribute to the early spring collections of immature Schizopoda. The June catches, however, may have been influenced by breeding Neomysis. In June 1941, large numbers of immature Schizopoda were caught in the southwest region where big catches of adult Neomysis had occurred from March to May. *Erythrops erythrophthalma* was the only other mysid in the Georges Bank plankton and its occurrence was sporadic. It was, however, always found beyond the 100 m. contour of the bank and usually beyond the 200 m. contour; hence, it may have contributed immature mysides to the March and April offshore catches.

The most abundant euphausiid in the Georges Bank plankton was *Thysanoessa inermis*. As previously discussed, adults were found on the bank during spring but disappeared with the onset of summer, either to avoid unfavorable physical conditions or because currents which might affect their distribution changed in strength. There is evidence that Thysanoessa breeds during spring; hence some of the large numbers of euphausiid larvae which occurred in the immature Schizopoda collection probably resulted from the breeding of this euphausiid. Few immature Schizopoda were caught in September, but many late calytopis stages of euphausiids and small, immature Thysanoessa were caught during this month. It is very doubtful that *Meganyctiphanes norvegica* breeds successfully on Georges Bank, for reasons previously mentioned, but it has a wide distribution in the gulf and occurs on the seaward slopes, hence the facts seem to indicate that while *Meganyctiphanes norvegica* and *Erythrops erythrophthalma* may contribute chiefly to the slope catches and *Neomysis americana* to the June central bank catches, immature Schizopoda on the bank are chiefly composed to juvenile *Thysanoessa inermis*. If this assumption is correct, then although adult Thysanoessa disappears in June, the animal does not fail to be

represented as a species on Georges Bank throughout the year. The adults may be absent but eggs and larvae remain to develop on the bank.

The vertical distribution of immature Schizopoda, shown by the plankton sampler catches, demonstrates that the animals occur most frequently in the second-depth stratum, although there is a tendency for them to migrate into the shallow stratum at night.

DECAPOD LARVAE

OCCURRENCES

On Georges Bank, decapod larvae were caught during January in very few tows and in small quantities. There was a decided increase in size of catches with the onset of spring (3 hauls of more than 500 per standard haul in May) but the occurrence of the larvae did not begin to increase sharply until June when they were taken at 22 stations, approximately twice as many as in May (Fig. 10). Results similar to these were found for the waters south of Cape Cod by Bigelow & Sears (1938). On Georges Bank, the larvae occurred chiefly within the 100 m. contour and many catches were made on the central area of the bank.

The larvae, characteristically concentrated in April and May when several catches of more than 1000 per standard haul were made, had become more evenly distributed by June when approximately 50% of the hauls were more than 100 per standard haul. This increase in average abundance suggests that by chance the spring tows had been made in areas where considerable hatching had previously taken place, and that in the meantime dispersal of the larval swarms had been accomplished, probably by the action of currents or other water movements. Wide fluctuation in numbers is a common characteristic of the occurrence of decapod larvae during spring. Throughout summer, decapod larvae undoubtedly occur on Georges Bank in considerable numbers since, when compared with June, the September catches indicated no reduction in quantity or extent of distribution.

Because egg-bearing *Crago septemspinosus* have been observed in May and June on Georges Bank, many of the decapod larvae in the Georges Bank collection can be attributed to this species. Late larval stages of Crago were identified in the plankton but no estimate of their number was taken. Several investigators have noted in New England and Canadian waters the abundance of *Crago septemspinosus* larvae in the plankton during summer (Bigelow

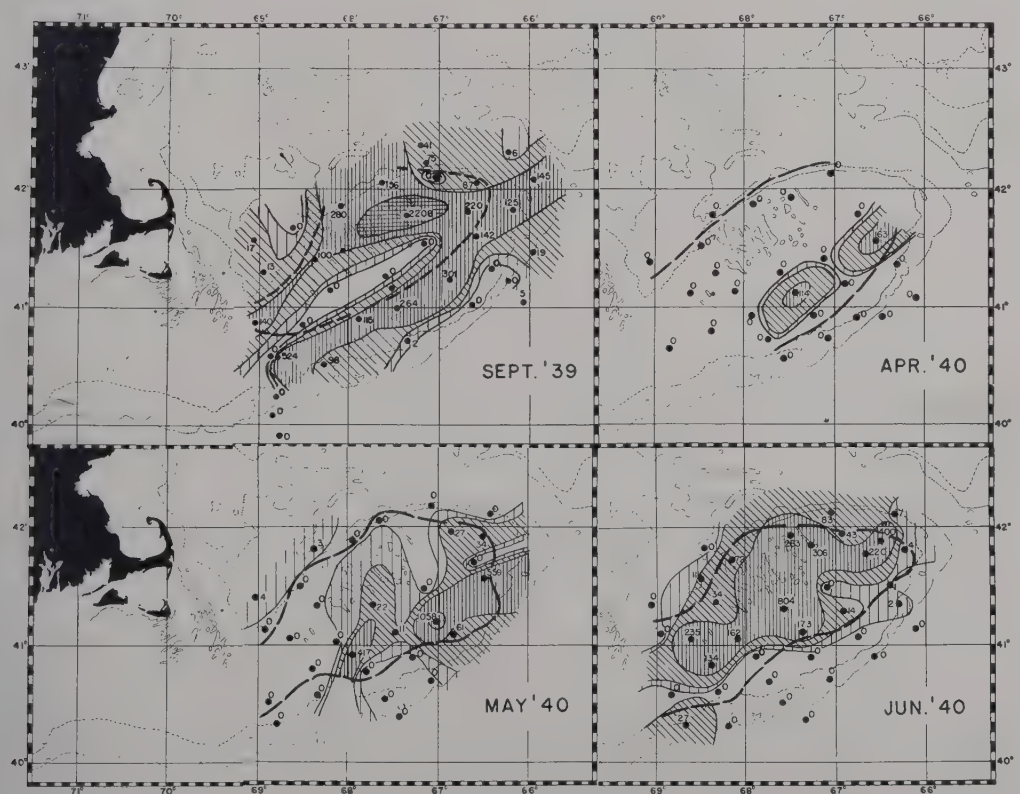

FIG. 10. Distribution of decapod larvae on Georges Bank for September 1939, April, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of the stramin net. Boundary of Mixed Area shown by heavy broken line.

1926, Fish & Johnson 1937; Bigelow & Spears 1939). Other decapods, however, such as several species of rock and hermit crabs are also known to live on Georges Bank and their larval stages also occur in the plankton (Smith & Harger 1874, Bigelow 1926). The larvae of crabs and other decapods have been reported to provide rich food for mackerel on Georges Bank (Kendall 1908).

Vertical distribution of decapod larvae caught by plankton sampler indicates that the crustaceans occur chiefly in the shallow stratum, although there is a slight tendency for them to sink into the second-depth stratum at night.

To conclude, a number of decapods probably contribute to the decapod larvae of Georges Bank. The larvae are found chiefly within the 100 m. contour of the bank and usually the largest catches are made on the central area. The larvae occur on the bank in considerable numbers throughout late spring, summer and fall, but are greatly diminished in occurrence during winter.

DISCUSSION

The larger crustacea of Georges Bank dealt with in this paper have been shown to be planktonic, at least during part of their life, hence their distribution will be affected in varying degrees by water movements. Redfield (1939) states "the geographical distribution of organisms in the sea is a hydrodynamic problem." The environment of specific regions will be determined by a complex balance of physical and biological factors. Of these factors flow of water is one of major importance affecting both the nature of the environment and the supply of organisms to it. The present knowledge of the physical oceanography of Georges Bank is limited because as yet, no satisfactory method of observing the complex and often sudden changes in such shallow water areas has been perfected. Ecological studies by biologists of animal communities within the Gulf of Maine and Georges Bank have contributed to the knowledge of the current systems of these areas (Redfield 1939, Clarke, Pierce, and Bumpus 1943), but for this purpose the larger Crustacea may be less satisfactory, since on the one hand, their swimming powers may not be as feeble as is usually supposed, and on the other, they may at times rest on the bottom and fail to indicate water movements there.

It is important to keep in mind that "bank" water is a mixture of Gulf of Maine and oceanic water and that the process of mixing is continuous although the rate may vary.

During summer Georges Bank is relatively well-stirred but is surrounded by more stable stratified water. There is little flow of water across the bank from the Gulf of Maine at this time since the peripheral current around the north and east margins is strong. Stability of the stratified layers surrounding the bank and also over the bank is probably at its maximum in September, hence vertical turbulence must be greatly suppressed compared to other seasons. Relatively heavy, saline water may be drawn up on the bank from seaward and pumped along its bottom, as it were, by each successive tidal wave. This water is mixed slowly with lighter, fresher water drawn into the central eddy from the Gulf of Maine. Mixed water would concurrently drain off the bank at different levels. These water movements may set in motion subsidiary eddies or counter currents.

For the colder months of the year little is known about the bank's circulation. Persistence of the population of *Sagitta elegans* throughout winter has been considered an index of permanence for at least part of the bubble of Mixed Area water (Clarke, Pierce, & Bumpus, 1943). Dynamic isobaths calculated by Watson (Redfield 1940, Fig. 10) suggest that as temperature falls with the onset of winter, contrast between bank water and the surrounding water masses may be so reduced that between January and March the peripheral current around the bank, formed by the Gulf of Maine eddy, practically disappears and Gulf of Maine water sweeps freely across Georges Bank. Isobaths are widely spaced for January showing that such water movement is slow. Heavy winter gales may have a dislocating effect on this type of water, forcing masses of it off shore. Although Iselin (1939) states that local gradient currents must be greatly reduced before winds can have marked effect, otherwise bank or coastal water would be blown seaward much more often than it is. During March and April isobaths indicate a slackening flow across the bank and gradual reestablishment of the peripheral current. Bigelow (1926) found the whole area of Georges Bank "dead water" in March. Presumably, as spring is succeeded by early summer, velocity and volume of the bank's peripheral current increases due to progressive incorporation of river water into the northwestern sides of the Gulf. Since water no longer flows across the bank lateral components again become more important factors in the mixing mechanism.

Thus there may be two phases, as it were, in the cycle of the mixing mechanism. During winter vertical turbulence is the predominant factor at work, but in summer and autumn when stability of the strafied layers is high, turbulence of this type is restricted to shoal areas and lateral mixing of water becomes the more important factor.

Distribution of *Monoculodes edwardsi, Neomysis americana* and *Crago septemspinosus* (Figs. 3, 5, 8) demonstrates that these organisms were present on Georges Bank throughout the eleven cruises. Failure to catch *Neomysis americana* in March 1940 as compared with March 1941 (Fig. 5) can be explained only by assuming either the organisms had perished for some reason or they were in a very localized swarm on the central bank which the March survey did not sample. Swarms of this type encountered in January and April, 1940 lend plausibility to such an assumption.

During spring, while numbers of individuals of these three species had decreased, their distribution

in the water mass remained about the same as before. Decline in relative numbers was probably due more to normal mortality, or to tidal mixing distributing the population more homogeneously than to dislocation of the water mass and its animal population by currents or gales. For, if the latter were the case, marked differences in distribution would likely result. Numbers of each species decreased towards the 200 meter contour, which indicates that the bank was not receiving additions to its stock from Gulf or offshore. Hence, occurrence of these species, which as adults are characteristic of bottom water, is thus either independent of currents set up by the mixing process or the movement of bottom water is too gradual to disperse them. Friction undoubtedly affects motion of bottom water and tends to increase its permanence.

Additional evidence for the permanence of at least certain layers of Georges Bank water is suggested by the development of *Thysanoessa inermis* and *Crago septemspinosus*. September catches of these crustaceans were composed chiefly of young stages, while January to March catches showed a steady increase in length of individuals (Tables 11, 12). These data show the same population of *Thysanoessa inermis* and *Crago septemspinosus* continued on the bank during fall and winter. Moreover, individuals from broods off the bank did not appear to have been introduced. Distribution of *Monoculodes edwardsi* and *Crago septemspinosus* indicated that extensive horizontal water movements or eddies in the bottom water of Georges Bank might be formed, nevertheless. There was no close similarity in the distribution of these two organisms for most of the year, beyond that already mentioned, but during spring in 1940 and 1941 both were unusual in having certain common features; the horizontal occurrence during April and May appeared to change from an irregular pattern to one with a well defined east and west group separated by an area having few or no individuals (Figs. 3, 8). These eddies may be associated with the initiation in spring of active lateral mixing.

History of the population of *Meganyctiphanes norvegica* and *Themisto compressa* during winter was different from any of the other crustaceans discussed inasmuch as these organisms were not found on Georges Bank at that season. Meganyctiphanes, relatively widespread in September, had disappeared from Georges Bank by January and was subsequently caught only at deep stations on the bank slopes (Fig. 7). Additional evidence for the general occurrence of adult Meganyctiphanes in the Gulf adjacent to Georges Bank was provided by tows made with a continuous plankton recorder (Hardy 1946). Beyond the 200 meter contour Meganyctiphanes was the only large crustacean caught by the recorder along the entire northern edge from March to June. Because Meganyctiphanes disappeared so completely during winter they were either swept away by flow of water across the bank, or they had then developed the ability to swim actively enough to avoid unfavorable environmental conditions, or they perished as a result of such conditions. Displacement of Meganyctiphanes, at least up to January, would not appear likely, at any rate *Themisto compressa* showed no sign of decrease at that time. Indeed, absence of adults of both species during winter and spring could hardly be attributed to water movement alone since the organisms were endemic to Gulf of Maine and bank slopes and at least some of those swept on and off the bank would be caught there. Available data, nevertheless, pointed to their absence. The physical state of the water that presented an unfavorable environment may have been responsible for their nonoccurrence. Several ecological factors were also undoubtedly involved, however, since, as already has been mentioned, the organisms were often caught only on the slopes during spring when comparable conditions existed on the central bank itself. Therefore, while temperature by itself may have been a limiting factor at certain extremes, a combination of influences, as yet imperfectly understood, probably affect the organism's distribution during winter and spring on Georges Bank.

To conclude, the characteristics and distribution of these species: *Monoculodes edwardsi, Crago septemspinosus,* and *Neomysis americana* indicate an endemic existence for them on Georges Bank. There was no evidence that the organisms were being carried to the bank from the surrounding areas. Individuals, bred in spring, maintain the bank population at a high level as adults through autumn and winter. Reduction in numbers is the normal result of mortality rather than loss by water movement. Hence bottom layers of water on Georges Bank appear to have considerable permanence even during winter, a season when the practically homogeneous water mass is most likely to be dislocated by gales or other dynamic agencies.

On the other hand occurrence during autumn of *Themisto compressa,* and *Meganyctiphanes norvegica,* animals endemic to Gulf and water surrounding the bank, contributes evidence for a mixing of water over the bank. In the stable, stratified layers surrounding it, the Georges Bank's mixing action may form frictional eddies or currents by which water is drawn towards the central mass of mixed water. The large numbers of immature animals of these species carried, apparently, by this inflowing water may have been drawn from Gulf of Maine and slope stocks by lateral turbulence. Absence during winter and spring of these organisms is believed due either to ability of adults to avoid in some way the drift to the bank and the unfavorable conditions which may exist there or they are carried to the bank only to perish quickly. Species such as *Themisto compressa* and *Meganyctiphanes norvegica* occur on Georges Bank, therefore, only as migrants. There is no evidence of local stocks.

Distribution and characteristics of *Thysanoessa inermis* suggest that it is intermediate between the endemic forms and the migrants. Water movements or physical conditions that disperse *Themisto compressa* or *Meganyctiphanes norvegica* do not affect it during late autumn and winter. Moreover, its dis-

tribution in March and April indicates *Thysanoessa inermis* may be circulating in eddies that have no obvious influence on the other two groups. Withdrawal of *Thysanoessa inermis* with the onset of summer has no clear relationship to flow of water off Georges Bank, inasmuch as the peripheral current is now well established around it. Hence, absence of *Thysanoessa inermis* in summer may be due either to death of adults after breeding or to withdrawal of the organisms from an unfavorable environment. Distribution of *Thysanoessa inermis* as compared with the other larger crustaceans emphasizes the individual differences that may exist among plankton of Georges Bank.

Distribution of *Sagitta elegans* studied by Clarke, Pierce, & Bumpus indicated that very small amounts of water were entering the Mixed Area from the south and east in September, whereas distribution of *Thysanoessa inermis, Meganyctiphanes norvegica* and *Themisto compressa* demonstrates either that lateral components were then contributing to the mixing mechanism or that these animals were reacting to a favorable environment and entering it by their own efforts. It is actually possible that both influences were at work. In the sagittae investigation it was also found that a tongue of water rich in Calanus, extending across the eastern end of Georges Bank and curving south, was a clear indication that a current from the Gulf was flowing over the southern margin of the bank. Distribution of *Themisto compressa* seems to check more closely with the probable path of this current than does the distribution of *Thysanoessa inermis* and *Meganyctiphanes norvegica*. Hence this current is probably surface water.

Thus, occurrences of the larger crustaceans on Georges Bank illustrate the complex relationships and varied character of the ecological factors governing distribution of animals on the bank. Possible effect of currents set up by the mixing mechanism on the distribution of several organisms have been described, yet it is realized that currents are baffling and elusive forces since they often change strength and direction with changing depth and are also affected by varying turbulence of wind. Techniques for measuring these changes have not yet been perfected. The effect of water temperature on distribution is also not entirely clear. The conclusions stated are suggested with these limitations in mind in the hope that they may serve a useful purpose in furthering the ecological study of Georges Bank.

SUMMARY

1. Assuming that 300 cubic meters of water was filtered during the standard haul of a stramin net, the range in average volumes of crustacean plankton on Georges Bank varied from a March-April minimum of 0.1 cc. per cubic meter to a June maximum of 0.6 cc. per cubic meter. Both maximum average volumes and maximum individual volumes occurred in June. Maximum individual catch was 1200 cc. per standard haul or approximately 4.0 cc. per cubic meter. These average volumes of plankton caught by the stramin net were found to compare favorably with more complete measurements of plankton made elsewhere on both sides of the Atlantic. Hence it is clear that Georges Bank supports a rich plankton.

2. Mackerel, herring, cod, and other commercially important fishes were shown to depend on the larger crustaceans or their larvae for much of their food. These crustaceans have therefore an important role in the food cycle of Georges Bank.

3. Tows from the region forming the long axis of the bank had the greatest volumes of plankton on all cruises. Presumably a number of factors, such as; type of bottom, moderate depth and physical state of the water, a rich and prolonged supply of phytoplankton (Sears 1941) combined to produce on this extensive area lying between the northern shoals and the 100 meter contour to the south an environment favorable for the breeding of the larger crustaceans.

4. Of the larger planktonic crustaceans on Georges Bank the predominating organisms in the stramin net collection were; *Monoculodes edwardsi, Themisto compressa, Pontogenia inermis Neomysis americana, Thysanoessa inermis, Meganyctiphanes norvegica, Crago septemspinosus, Dichelopandulus leptocerus,* Schizopoda immature, decapod larvae.

5. With the exception of *Meganyctiphanes norvegica* and *Dichelopandulus leptocerus* the crustaceans were usually caught inside the 100 meter contour of the bank.

6. The amphipod *Monoculodes edwardsi* showed the greatest average abundance and widest distribution of all the species in the plankton collection. It was taken at approximately 60% of the hauls and of all species had the highest average number per standard haul per cruise for seven of the eleven cruises.

7. The species next most widely distributed and generally abundant were *Crago septemspinosus* and *Meganyctiphanes norvegica,* which occurred in not less than 10% of all hauls and had an average of one or more per standard haul for each cruise.

8. *Neomysis americana* occurred in the largest swarms but showed marked fluctuations in abundance. Individual catches up to 15,000 per standard haul were made when in adjacent areas under apparently similar physical conditions catches were small.

9. Although never occurring in the plankton as abundantly as the mysid *Neomysis americana* or the amphipod *Monoculodes edwardsi,* the large size and bulk of the euphausiids *Thysanoessa inermis* and *Meganyctiphanes norvegica* or the decapods *Crago septemspinosus* and *Dichelopandulus leptocerus* must be considered in order to estimate their true role in the food cycle of the bank. Each of these crustaceans would be approximately four to six times the size of the previously mentioned smaller species.

10. A seasonal variation in occurrence was shown by *Pontogenia inermis, Themisto compressa,* decapod larvae, Schizopoda immature which were caught most frequently during spring and summer; *Thysanoessa inermis,* during autumn and winter; *Meganycti-*

phanes norvegica and *Dichelopandulus leptocerus,* during autumn. *Neomysis americana* avoided both the coldest and the warmest periods of the year.

11. Breeding during spring and summer was common for many of the larger planktonic crustaceans. *Thysanoessa inermis* and *Neomysis americana,* however, probably bred only during spring; while *Meganyctiphanes norvegica* presumably did not breed at all on the bank.

12. With the possible exception of *Dichelopandulus leptocerus,* which may live three years, the larger crustaceans are believed to have a one year life-cycle.

13. Vertical distribution of the organisms showed that the majority were caught in the second depth stratum, with the exception of *Thysanoessa inermis* and *Themisto compressa* caught more often in the shallow stratum, though not necessarily on the shoal areas of the bank.

14. *Monoculodes edwardsi, Thysanoessa inermis,* and *Meganyctiphanes norvegica* showed some tendency to move into the shallow stratum at night. *Meganyctiphanes norvegica* was never taken in the shallow stratum by day, the other two species were sometimes caught there equally well by day or night. There was no other marked vertical migration during day or night.

15. Many of the larger crustacea were caught both inside and outside the Mixed Area. They therefore tolerate a moderately broad range of temperatures and salinities. Species largely confined within the Mixed Area were *Pontogenia inermis,* caught where temperature varied from 5° C. to 10° C., and *Neomysis americana,* which preferred a 4° C. to 5° C. temperature range. Concerning the effect on distribution of variations in food supply or the nature of the bottom little at present is known.

16. Invariably caught outside the Mixed Area were *Meganyctiphanes norvegica* and *Dichelopandulus leptocerus. Meganyctiphanes norvegica,* while a creature of the banks on both sides of the Atlantic, usually withdrew from extremes of temperature or salinity. Apparently it avoided areas having temperatures below 3° C. and above 16° C. *Dichelopandulus leptocerus* appeared to be a benthonic decapod that preferred cold water.

17. Distribution of *Monoculodes edwardsi, Neomysis americana* and *Crago septemspinosus* on Georges Bank showed them to be endemic there, thus indicating that the deep stratum, irrespective of the boundaries of the Mixed Area, could have permanence during winter and spring, although extensive eddies might occur in it. This finding is an extension of the suggestion of Clarke, Pierce, & Bumpus that the homogeneous water on Georges Bank may have permanence from season to season.

18. Distribution of *Thysanoessa inermis* indicated that young stages either hatched from local spawning or else drifted to the bank during spring and summer. Adults present during winter months were absent in spring. They may have died after breeding or have been dispersed by changes in the physical environment. Water movement was not obviously an important limiting factor. *Themisto compressa* and *Meganyctiphanes norvegica* also appeared to be migrants, drifting as juveniles to central Georges Bank in late summer and autumn. Adults were caught only on the bank's margin during winter and spring.

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Contribution No. 398

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INDUSTRIAL AND ENGINEERING CHEMISTRY,
Vol. 40, Page 249, February, 1948
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ACTION OF ANTI-FOULING PAINTS

V. Use of Glycine Solutions as Accelerated Test of Availability of Toxic[1]

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An antifouling paint which depends on copper or one of its compounds dissolves in an alkaline glycine solution about 100 times as fast as in the sea. The results of immersion for three days in the glycine solution predicts whether the paint will maintain a copper leaching rate adequate to prevent fouling when immersed in the sea. Satisfactory results are obtained with paints containing metallic copper or cuprous oxide as a toxic, whether the paint depends on a soluble matrix or on continuous contact of toxic particles to permit the toxic release. This accelerated test permits the elimination of unsatisfactory formulations without time-consuming and expensive exposures in the sea. A large number of variations of a given paint formulation can thus be evaluated quickly.

PREVIOUS papers have shown that antifouling paints, which depend on copper or one of its compounds for their toxicity, must release copper at a rate of at least 10 micrograms per square centimeter per day to prevent the attachment of fouling organisms (*8*). The ability of a paint to maintain an adequate leaching rate for long periods depends both upon the solubility of the toxic compound (*4, 6*) and upon the nature of the matrix. An insoluble impermeable matrix may be used if the loading with the toxic pigment is adequate to ensure continuous contact of the toxic particles throughout the film (*5*). Lower toxic loadings may be used in a paint containing soluble matrix constituents, since the dissolution of the matrix exposes the deeper stores of toxic (*7*). The determination of leaching rates or of fouling resistance will

[1] Previous papers in this series appeared in 1946 INDUSTRIAL AND ENGINEERING CHEMISTRY on pages 612, 699, 806, and 931.

show whether a paint is satisfactory, but these tests require prolonged exposures in the sea. An accelerated test to eliminate those paints which will not release toxic at an adequate rate is valuable in studying and developing effective formulations.

A test is described in this paper which uses an alkaline solution of glycine to accelerate the dissolution of the paint. The dissolution of copper from the paint is accelerated by the formation of the highly soluble cupric glycinate complex ion (*1*). The alkalinity of the solution, maintained by the buffering property of sodium glycinate, accelerates the dissolution of acidic resins of the matrix. Copper antifouling paints with soluble matrices dissolve in the appropriate glycine solution approximately 100 times as fast as in steady-state leaching in the sea. The dissolution of copper from paints with insoluble matrices, having the toxic particles in continuous contact, is similarly accelerated in this solution.

TABLE I. DISSOLUTION OF COLD PLASTIC PAINT IN SOLUTIONS CONTAINING 0.48 MOLE SODIUM CHLORIDE AND VARIOUS AMOUNTS OF GLYCINE AND SODIUM HYDROXIDE

(One panel, 155 sq. cm. in area, in a liter of solution for 48 hours)

Compn. of Solvent, Moles/L. × 10^3				Paint Dissolved, μg./Sq. Cm./Day		Ratio, Cu_2O:	Acceleration
Glycine	NaOH	Excess	Initial pH	Cu_2O	Matrix	Matrix	Factor
5	5	0	10.3	225	205	1.1	20
5	10	5	11.0	142	..	..	12
5	25	20	11.3	342	..	..	30
5	50	45	11.4	324	..	..	28
5	100	95	11.4	251	..	..	22
10	10	0	10.4	790	540	1.5	69
25	25	0	10.6	2050	970	2.1	178
25	25	0	10.5	2250	1850	1.2	195
25	30	5	11.0	2050	1900	1.1	178
25	50	20	11.3	710	1620	0.44	62
25	75	50	11.5	515	1570	0.33	45
50	50	0	10.8	2100	1020	2.0	183
100	100	0	10.9	2020	1250	1.6	175

TABLE II. COPPER AND MATRIX DISSOLVED BY GLYCINE SOLUTION AND COPPER LEACHING RATES OF PAINTS CONTAINING GRADED AMOUNTS OF CUPROUS OXIDE IN COLD PLASTIC MATRIX

Cu_2O in Dry Paint, Vol. %	Glycine Extract[a], Mg./Sq. Cm.		Cu Leaching Rates, μg./Sq. Cm./Day after					
	Cu	Matrix	2 mo.	3 mo.	4 mo.	5 mo.	6 mo.	Av.
18	3.95	1.48	16	14	10	7	7	11
14	3.42	1.72	12	12	10	7	7	9.6
12	2.47	1.31	10	8	7	7	7	7.8
9	2.22	1.57	8	8	8	5	6	7.0
6	1.44	1.69	8	7	6	6	4	6.2
3.6	0.86	1.64	6	4	4	5	4	4.6

[a] One panel, 155 sq. cm. in area, in 1 liter containing 0.025 *M* sodium glycinate and 0.048 *M* NaCl for 72 hours.

COMPOSITION OF GLYCINE SOLUTION

The solvent action, pH, and buffering capacity of the solution depend upon the concentration and proportions of glycine and sodium hydroxide. The selection of the test solution may be based on the following criteria: (*a*) The ratio of dissolved toxic

and matrix should approximate their proportions in the paint. This requirement corresponds to the theoretical dissolution of paints with soluble matrices in the sea, although experiments indicate that, in many paints, the toxic is dissolved in relative excess of its proportion in the paint (7). (*b*) The acceleration should be adequate to dissolve, in a few days, a thickness of paint equivalent to that which would dissolve in the sea during six months to one year of exposure.

The effect of varying the composition of the glycine solution on the amount of copper and matrix dissolved from a cold plastic paint is shown in Table I. The solutions contained various amounts and proportions of glycine and sodium hydroxide. Sodium chloride was included in all solutions at a concentration equal to that of the sea water accepted as standard for the leaching rate test (17 parts per thousand or 0.48 *M*).

The paint used contains 34% rosin and 41% cuprous oxide in the dry paint—that is, a ratio of cuprous oxide to soluble matrix of 1.2:1. The ratio dissolved varies between 0.33 and 2.1:1. The lower values are obtained when excess base is present, since this increases the dissolution of the matrix and decreases the dissolution of cuprous oxide. The use of excess base has another disadvantage—namely, it may so soften the paint film that the latter falls from the panel. The solution used should, therefore, contain equimolar parts of glycine and sodium hydroxide.

The acceleration factors in Table I were obtained by dividing the rate of extraction in the glycine solution by the steady-state leaching rate in the sea. Leaching rates have been determined on seventeen samples of the paint used in this experiment. The average of the leaching rates between the second and sixth month of exposure, inclusive, give a steady-state leaching rate of 11.5 micrograms of cuprous oxide per square centimeter per day. The acceleration factors for the different glycine solutions range from 12 to 195. In the solutions containing no excess base the rate of dissolution of the paint increases as the sodium glycinate is increased. Above a concentration of 0.025 *M* no further increase in the rate of dissolution of cuprous oxide is obtained, although the dissolution of the matrix increases up to a concentration of 0.1 *M* (Figure 1).

The solution containing 0.025 mole sodium glycinate per liter with no excess base was selected as the standard test solution. This dissolved cuprous oxide and matrix at a ratio of 1.2 and 2.1:1 in two tests and the acceleration factor for the paint tested was almost 200.

According to Borsook and Thimann (*1*), the complex formed at pH values between 8 and 12 contains two moles of glycine combined with one mole of copper. This solution will combine, therefore, with about 800 mg. of copper per liter. Under the conditions of the test to be defined, this is more than 5000 micrograms per square centimeter of paint surface. This is equivalent to a uniform leaching rate of 10 micrograms per square centimeter per day maintained for five hundred days.

MATERIALS AND METHODS

A ground glass panel 3 × 4 inches in size (155 sq. cm.) is painted on both sides, dried 4 days, and extracted for 72 hours in a liter of a solution containing 0.025 *M* sodium glycinate (obtained from Dow Chemical Company) and 0.48 *M* NaCl (pH = 10.5). The solution is agitated by bubbling air, delivered at the base of the panel by a glass tube of 7-mm. inside diameter, at a rate of 10 or more bubbles per second.

The copper content of the solution is determined by the carbamate analysis (*2*, *3*), after appropriate dilution, if the concentration is less than 100 mg. per liter. Larger concentrations are analyzed by direct photometry of the blue color. Sodium glycinate must be present in excess to develop the maximum color. An equal volume of 1.5 *M* sodium glycinate is therefore added to the aliquot for analysis. The solution is read in a Klett Summerson photometer using a red filter with a spectral transmission range of 640–700 millimicrons. The copper solution used to calibrate the photometer is also made up in the sodium glycinate test solution and treated like the unknown sample.

The matrix is extracted from the acidified test solution with ether. The ether extract is washed with distilled water, dried, and weighed.

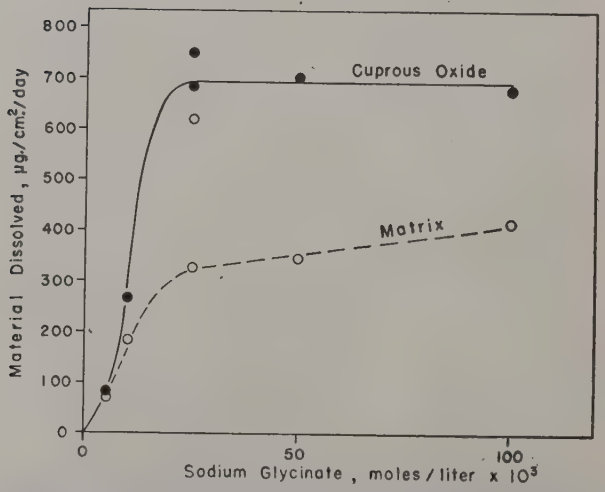

Figure 1. Amounts of Cuprous Oxide and of Matrix Dissolved from Cold Plastic Paint by Solutions Containing 0.48 *M* NaCl and Various Concentrations of Sodium Glycinate

TABLE III. COPPER AND MATRIX DISSOLVED BY GLYCINE SOLUTION AND COPPER LEACHING RATES OF PAINTS CONTAINING GRADED AMOUNTS OF METALLIC COPPER FLAKE IN MATRIX CONSISTING OF 3 PARTS ROSIN TO 1 PART VINYLITE (VYHH)

Cu in Dry Paint, Wt. %	Glycine Extract[a], Mg./Sq. Cm.		Cu Leaching Rates, μg./Sq. Cm./Day after					
	Cu	Matrix	2 mo.	3 mo.	4 mo.	5 mo.	6 mo.	Av.
76	4.63	1.17	11	11	17	19	17	15.0
57	4.14	1.36	10	11	13	16	12	12.4
38	2.44	1.34	11	8	9	7	5	8.0
27	2.08	1.34	10	7	8	6	4	7.0
19	1.39	1.39	9	4	9	3	2	5.4
11	1.26	1.91	4	2	2	1	1	2.0
8	0.66	1.70	9	3	3	1	1	3.4
4	0.59	2.63	4	2	5	3	2	3.2

[a] One panel, 155 sq. cm. in area, in 1 liter containing 0.025 *M* sodium glycinate and 0.048 *M* NaCl for 72 hours.

TABLE IV. COPPER AND MATRIX DISSOLVED BY GLYCINE SOLUTION AND COPPER LEACHING RATES OF PAINTS CONTAINING VARIOUS PROPORTIONS OF ROSIN AND ESTER GUM IN MATRIX

Rosin, %	Matrix Compn.[a] Ester Gum, %	Glycine Extract[b], Mg./Sq. Cm.		Cu Leaching Rates, μg./Sq. Cm./Day after					
		Cu	Matrix	2 mo.	3 mo.	4 mo.	5 mo.	6 mo.	Av.
25	0	4.43	1.97	18	16	15	14	14	15.4
24	1	4.19	1.68	17	10	12	13	14	13.2
22.5	2.5	3.07	1.61	9	7	8	8	11	8.6
19	6	2.82	1.35	6	4	5	5	7	5.4
16.5	8.5	2.43	1.15	5	3	5	4	5	4.4
12.5	12.5	2.50	0.92	5	3	4	3	5	4.0
6	19	0.08	0.43	2	1	3	1	2	1.8
0	25	0.15	0.12	2	1	3	2	2	2.0

[a] These paints also contain 12.5% Arochlor 1254 and 62.5% cuprous oxide by weight.

[b] One panel, 155 sq. cm. in area, in 1 liter containing 0.025 *M* sodium glycinate and 0.048 *M* NaCl for 72 hours.

GLYCINE EXTRACTS OF TYPICAL PAINT

The dissolution of copper by the glycine solution depends upon the same properties of the paint which determine its copper leaching rate in the sea. Variations in the amount of cuprous oxide or copper in the formulation, or variations in the composition of the matrix, will affect the amount of copper dissolved under either condition.

The effect of the cuprous oxide content of a cold plastic paint on the dissolution of the paint in glycine and on the leaching rate after exposure in the sea is illustrated in Table II. The pigment volume of these paints was kept constant by the substitution of Celite for the cuprous oxide removed. As the cuprous oxide content of the paint is decreased, the copper leaching rate in the sea and the amount of copper extracted in the standard glycine solution both decrease. The amount of matrix dissolved in the glycine solution is substantially the same for all of the paints, as would be expected, since its volume and composition were unchanged.

That the glycine solution accelerates the dissolution of metallic copper paints is shown by the data of Table III. As the copper flake pigmentation of this paint is increased, both the copper leaching rates in the sea and the copper dissolved in the glycine

solution increase. The proportion of matrix in the paints increased as the copper was decreased. The increase in the amount of matrix dissolved by the glycine solution reflects this increase.

The substitution of an insoluble resin for the rosin of a soluble matrix paint (7) also decreases the copper dissolved in glycine or in the sea. An example of this effect is shown in Table IV for a series of paints in which ester gum was substituted for various parts of the rosin of the matrix. The amount of copper and matrix dis-

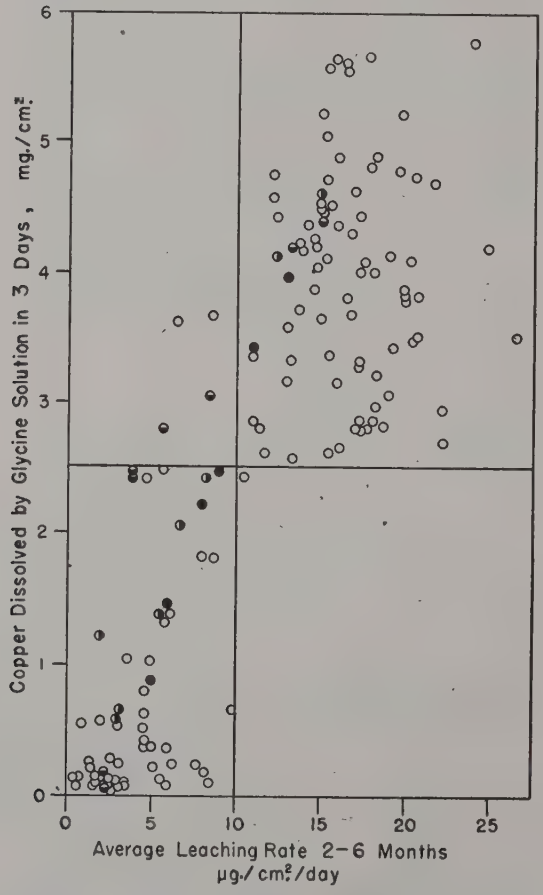

Figure 2. Amount of Copper Dissolved by Glycine Solution Compared to Steady-State Copper Leaching Rate in Sea of a Variety of Copper Antifouling Paints

● Data from Table II
◑ Data from Table III
◒ Data from Table IV

solved in the glycine solution from these paints decreased as the ester gum content of the paint increased. A sixteen fold difference was observed in the amount of matrix dissolved from these paints. This is in contrast to the data in Table II where the amount of matrix and its composition was the same for all of the paints and little change was observed in the amount of matrix dissolved, and to the data in Table III where the increase in amount of matrix resulted in only a twofold increase in the amount of matrix dissolved.

CORRELATION BETWEEN GLYCINE RESULTS AND LEACHING RATE TESTS

The value of the glycine solution as an accelerated test of antifouling paints lies in the degree to which the results correlate with leaching rates. During the course of two years' study this comparison has been made for several hundred formulations. The results show that the majority of the paints from which the glycine solution dissolves appreciable amounts of copper are able to maintain adequate leaching rates for long periods of immersion. The glycine test may be taken as indicating, therefore, whether an adequate mechanism for the release of the toxic is provided in the paint.

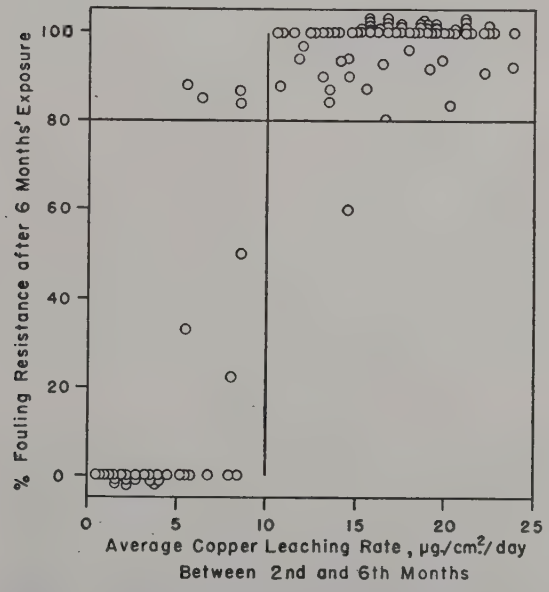

Figure 3. Fouling Resistance after 6 Months Compared to Steady-State Copper Leaching Rates of a Variety of Copper Antifouling Paints

To permit presentation of all the data, some points for 100% fouling resistance are plotted above the 100% line, and for 0% fouling resistance below the correct line. These points should be read as 100% or 0%, respectively.

The correlation between the copper dissolved in the glycine solution and the leaching rates of the paints, averaged between the second and sixth month of sea immersion, is given in Figure 2 for 146 paints. The paints described in Tables II, III, and IV are included. The remaining paints are of assorted compositions, including commercial paints and experimental paints designed and tested for the Navy Department. Some of the paints are pigmented with metallic copper, others with cuprous oxide. Some of the paints have soluble matrices; others are formulated with insoluble impermeable matrices (*5*, *7*). All of the paints of this miscellaneous assortment show a direct correlation between the copper dissolved in the glycine solution and the average copper leaching rate in the sea.

The criteria of a satisfactory performance for a paint, as drawn in Figure 2, are an average, steady-state copper leaching rate in sea water of 10 micrograms per square centimeter per day and a release of copper in the glycine solution in three days of 2.5 milligrams per square centimeter (833 micrograms per square centimeter per day). Taking these values, 83 of the 146 paints gave adequate results in both tests, and 58 gave inadequate results in both. For 96.5% of these paints, therefore, the glycine test, in three days, predicted accurately whether the average copper leaching between the second and sixth months of sea immersion would or would not be adequate. Four paints had leaching rates less than 10 micrograms per square centimeter per day, although the copper released in the glycine solution was greater than 2.5 milligrams per square centimeter; one paint had a leaching rate of 10.6 micrograms per square centimeter per day, although it released only 2.4 milligrams per square centimeter in the glycine test.

The glycine test does not accelerate the solution of copper to the same degree for all paints. Among the formulations giving adequate results in both tests the acceleration factors observed range from 41 to 130. Greater variation is obtained if the unsatisfactory paints are included. It follows that the absolute value for the steady-state copper leaching rate cannot be predicted from the results of a glycine test. The test does, however, indicate whether adequate leaching rates in sea water will be maintained.

DISCUSSION

The greatest utility of an accelerated test, such as the glycine test, is in studying modifications of a given formula in order to determine the suitability and proportion of new or changed ingredients. One can quickly eliminate modifications which have destroyed the ability of the paint to maintain an adequate leaching rate, and select those modifications which are worthy of the more extensive and time-consuming leaching rate and fouling exposure tests. The glycine test can be used in any laboratory, since seaside facilities are not required.

The glycine test should not, however, be expected to replace exposure of antifouling paints in the sea. It does not predict the value of the leaching rate nor the effective life of the paint. It is also conceivable that some formulations or ingredients may

necessitate the use of a different criterion for satisfactory performance in the glycine test because of differences in the accelerations of the dissolution of the paint.

The discussion in this paper has centered on the relation between the copper dissolved in glycine and the copper leaching rate, since these are related chemical characteristics of the paint. It is clear that an extension of the results of the glycine test to predict the performance of the paint in the sea rests on the validity of the leaching rate test. It is desirable, therefore, to review the available published information and to present additional data showing the degree of correlation between the copper leaching rate of the paint and the fouling resistance in the sea.

In a previous paper (*8*) some data were presented which indicated that the copper leaching rate of the paint must be about 10 micrograms per square centimeter per day in order to prevent fouling attachment. Additional previously unpublished data are included in Figure 3, which confirms the selection of this value as the critical one. In this figure the fouling resistance after six months' exposure is plotted against the copper leaching rates averaged between the second and sixth months of exposure. Like that of the paints in Figure 2, these data represent a miscellaneous assortment, some of which contain metallic copper, some cuprous oxide; some have soluble matrices, some insoluble matrices. Of the seventy-four paints having average leaching rates greater than 10, seventy-three rated 80% or more in fouling resistance. Of the thirty-three having average leaching rates less than 10, twenty-nine rated less than 80% in fouling resistance. It appears, therefore, that for this group of paints the leaching rate is an accurate indication of the ability of the paint to prevent fouling in about 95% of the tests.

Paints with certain types of leaching behavior were excluded from the above treatment. These include paints demonstrating variable leaching rates in which the average leaching rate might be high, although individual determinations are frequently low enough to permit fouling. Paints with poor physical character, particles of which may be washed off in the water of the leaching bath, are also excluded. Such paints generally give high apparent leaching rates, since the rate of dissolution from the detached particles is excessive, without being able to prevent fouling when immersed in the sea. Paints which depend upon other compounds for their toxicity—that is, mercury paints—are also excluded, since these paints may give adequate fouling resistance independent of their copper content or leaching rate. With these exceptions the copper leaching rate almost invariably shows a direct correlation with the fouling resistance of the paint.

Based on this comparison it is apparent that the glycine test can be used to predict the antifouling performance of a paint exposed in the sea. It will, in practically all cases, indicate the paints which will be unable to prevent the attachment and growth of fouling. These can then be eliminated from further tests. It should not, however, be used to predict which of a group of paints would be expected to give the best service. This can be determined only by exposures of the paints in the sea and their performance on ships in service.

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RECEIVED December 11, 1946. Contribution 398 of the Woods Hole Oceanographic Institution. These experiments were conducted under contract with the Bureau of Ships, U. S. Navy Department, which has given permission for their publication. The opinions presented here are those of the author and do not necessarily reflect the official opinion of the Navy Department or the naval service at large.

PRINTED IN U. S. A.

Contribution No. 399

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INDUSTRIAL AND ENGINEERING CHEMISTRY,
Vol. 40, Page 2124, November, 1948
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Action of Antifouling Paints

VI. EFFECT OF NONTOXIC PIGMENTS ON THE PERFORMANCE OF ANTIFOULING PAINTS

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PREVIOUS papers of this series (*3–6*) have discussed the properties of toxic pigments and of paint matrices which are important in formulating antifouling paints. The effects of adding nontoxic pigments to paints formulated both with soluble and insoluble matrices are described here.

The use of a nontoxic pigment introduces a third related variable in the paint composition. Any variation in one of the components, matrix, toxic pigment, or nontoxic pigment, must be compensated by a related variation of one or both of the other components. For experimental purposes it is convenient to maintain either the weight or the volume occupied by the toxic pigment constant so that comparisons between paints may be made. The nontoxic pigment is, then, substituted for an equal weight or volume of the matrix.

It has been shown by Young, Schneider, and Seagren (*8*) that the substitution of a nontoxic pigment for an equal weight of vehicle improves the antifouling effectiveness of a copper paint. This effect was attributed to an increase in the permeability of the paint film. The authors of the present paper found results with paints compounded with insoluble matrices confirm these observations. However, the increase in the availability of toxic is attributed to the increase in the volume which it occupies in the paint film when the nontoxic pigment is substituted in this way. As has been shown by Ferry and Ketchum (*4*), the probability of continuous contact of toxic particles increases, with a consequent increase in the leaching rate, as the volume occupied by the toxic in the paint increases. This is a purely geometrical effect which does not imply any change in the structure of the film or the manner of arrangement of the particles within it.

The inclusion of nontoxic pigments in antifouling paints formulated with insoluble matrices does not affect the leaching rates or fouling resistance provided the proportion, by volume, of the toxic pigment in the dry paint film is greater than the minimum critical value. In paints formulated with a soluble matrix, on the other hand, the introduction of a nontoxic pigment results in higher leaching rates at equal toxic volume fractions. Above a minimum critical toxic volume fraction, however, the fouling resistance is satisfactory regardless of the presence or absence of the nontoxic pigment. Variations in the total pigment volume fraction from 0.12 to 0.24 had little or no effect on the physical performance of these paint films when exposed in the sea. In the design of antifouling paints, therefore, it is necessary to determine first the critical toxic volume fraction required to give satisfactory antifouling performance. The total pigment volume can then be varied at will by the substitution of nontoxic pigments for an equal volume of matrix to obtain the most satisfactory paint.

MATERIALS AND METHODS

The Vinylite paints used in this investigation were compounded with materials supplied by the Bakelite Corporation—namely, cuprous oxide (electrolytic), polyvinyl chloride—acetate (Vinylite VYHH), and Celite. The varnish vehicle paints were supplied by Richard J. Eckart of the Sapolin Company, Inc. The varnish vehicle has the following composition:

25 lb.	BR-254 (phenolic resin)
75 lb.	Cumar V-2½ (cumarone resin)
3 gal.	Linseed oil
3 gal.	Wolin (Zapon K, a wood oil substitute)
10½ gal.	Solvesso 2
7 gal.	High flash naphtha
Trace of driers	

The soluble matrix paints were modifications of Navy Specification 52-P-61 paints formulated and supplied by the Mare Island Naval Shipyard. The leaching rates were determined by the standardized technique described in a previous paper (7). The exposures for fouling tests were made at Miami Beach, Fla., by Charles M. Weiss.

VINYLITE PAINTS

The leaching rates, during exposure in the sea, of a series of paints containing various amounts of cuprous oxide in Vinylite are given in Table I. Three paints in which Celite has been substituted for an equal weight of Vinylite are included. Comparison of the paints containing the same weight percentage of cuprous oxide shows that this substitution of Celite has appreciably increased the leaching rates.

The volume fraction occupied by the toxic pigment is also included in Table I. The substitution of Celite for an equal weight of Vinylite results in an increase in the proportion by

TABLE I. LEACHING RATES OF PAINTS CONTAINING VARIOUS AMOUNTS OF CUPROUS OXIDE AND CELITE IN VINYLITE

Paint Composition Weight, %			Cu_2O Volume	Copper Leaching Rates after Soaking, Weeks					Total Cu Leached,
Vinylite	Cu_2O	Celite	Fraction[a]	8	12	16	20	24	Mg./Sq. Cm.[b]
10	90	..	0.65	61	29	20	14	9	2.7
20	80	..	0.45	39	23	17	11	8	2.1
30	70	..	0.33	16	9	7	5	3	0.9
40	60	..	0.24	2	1	..	..	..	0.1
60	40	..	0.12	2	1	..	..	..	0.1
15	70	15	0.40	33	17	10	8	5	1.5
20	60	20	0.30	16	10	6	5	3	0.8
25	50	25	0.22	7	6	3	2	2	0.4

[a] The following bulking values were used in computing the volume fraction: Cu_2O, Grade 1, 0.0209 gal./lb., Vinylite, VYHH 0.098 gal./lb. and Celite 0.052 gal./lb.

[b] Calculated by integration of leaching rate-time curve, assuming a linear change between each pair of measurements.

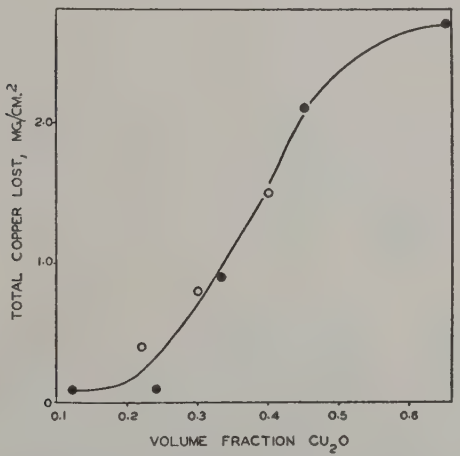

Figure 1. Total Amount of Copper Lost from Vinylite Paints Plotted against Volume Fraction of Cuprous Oxide in Paint

● **Paints that contain only cuprous oxide**
○ **Paints that also contain Celite**

volume of the toxic pigment in the dry paint film. For example, the volume fractions of the toxic in the two paints containing 70% cuprous oxide by weight are 0.33 for the paint with toxic alone, and 0.40 for the paint which also contains Celite. When the total amount of copper lost from the paints between the 8th and 24th weeks is plotted against the volume fraction of cuprous oxide, as in Figure 1, it is found that the availability of the toxic is directly related to the volume fraction of the toxic, and appears to be largely independent of the presence of Celite in the formulation.

The solution of copper from cuprous oxide paints made with a Vinylite vehicle depends upon the continuous contact of toxic

TABLE II. COPPER LEACHING RATES OF VARNISH VEHICLE PAINTS CONTAINING VARIOUS AMOUNTS OF CUPROUS OXIDE AND METALLIC COPPER

	Toxic Composition		Copper Leaching Rates, γ/Sq. Cm./Day after:				
	Weight %	Volume fraction[a]	0 mo.	1 mo.	2 mo.	3 mo.	4 mo.
Cu_2O	85	0.50	41	25	20	22	..
	82	0.45	36	18	15	14	..
	79	0.40	20	10	8[b]	9[b]	..
	75.2	0.35	39	5[b]	4[b]	7[b]	4[b]
	70.5	0.30	32	3[b]	3[b]	5[b]	3[b]
	65.0	0.25	30	2[b]	3[b]	4[b]	2[b]
	58.5	0.20	29	2[b]	2[b]	3[b]	2[b]
	50	0.15	22	2[b]	2[b]	3[b]	1[b]
Cu	80	0.35	215	30	23	37	22
	76	0.30	226	27	22	37	20
	71	0.25	229	25	17	31	14
	65	0.20	205	15	13	22	12
	57	0.15	193	4[b]	6[b]	10[b]	8[b]
	49	0.115	175	3[b]	3[b]	7[b]	4[b]

[a] Following bulking values were used in computing volume fraction: Cu_2O, Grade 2, 0.0197 gal./lb., Cu 0.015 gal./lb., varnish solids 0.111 gal./lb.
[b] Paint fouled at this time when exposed at Miami Beach, Fla.

particles. To obtain adequate contact the volume fraction occupied by the toxic must exceed 0.3 (*4*). The usefulness of Celite in improving the leaching rates of these paints appears to be related to the change in the volume fraction occupied by the toxic. The increase of this fraction results, when Celite is substituted for an equal weight of matrix, because the Celite is denser, and thus occupies less space than the equal weight of Vinylite which it replaces.

VARNISH VEHICLE PAINTS

The effect of nontoxic pigments on the availability of both cuprous oxide and metallic copper flake from a varnish vehicle paint of short oil length has been studied. It is necessary to know the minimum loading for both toxic pigments in this vehicle in order to evaluate the effects of the nontoxic pigment. The results of an experiment performed to determine this minimum loading are shown in Table II. Cuprous oxide must occupy a volume fraction greater than 0.35 in order to permit the release of the toxic pigment at an adequate rate to prevent fouling. This loading is somewhat greater than that which was found previously for Vinylite vehicles (*4*). When metallic copper is used as the pigment a toxic volume fraction of 0.20 or greater is adequate. The effectiveness of metallic flake pigments at lower loadings than are required for cuprous oxide has also been observed with other types of vehicles. It is suggested that the explanation may depend upon the geometric arrangement of the pigment particles. The cuprous oxide paints may be described as "cannon ball" structures in which one particle is piled upon another, roughly like the familiar structure of a pile of cannon balls. The pigment in the copper flake paints, on the other hand, may be arranged like a "house of cards." The latter arrangement would provide continuous contact with a lower pigment volume than the former.

TABLE III. EFFECT OF SUBSTITUTING CHINA CLAY FOR AN EQUAL VOLUME OF MATRIX ON COPPER LEACHING RATES OF VARNISH VEHICLE PAINTS CONTAINING A TOXIC VOLUME FRACTION OF 0.30[a]

Weight Composition[b]			Leaching Rates γ/Sq. Cm./Day after:				
Toxic	Inert %	Toxic %	0 mo.	1 mo.	2 mo.	3 mo.	4 mo.
Cu_2O	0	70	32	3[c]	3[c]	5[c]	3[c]
	6.6	67.4	44	3[c]	2[c]	5[c]	3[c]
	12.7	64.3	40	4[c]	3[c]	5[c]	3[c]
	18.3	61.7	50	5	4[c]	8[c]	4[c]
	23.3	58.7	59	5	5[c]	8[c]	5[c]
Cu	0	77	226	27	22	37	20
	5	74	218	44	19	37	16
	10	72	200	24	20	28	15
	15	69	235	27	23	19	19
	19	67	242	25	24	18	16

[a] Bulking value of china clay is 0.046 gal./lb. Other bulking values used are given in Table II.
[b] Varnish solids make up remainder of dry film.
[c] Paint fouled at this time when exposed at Miami Beach, Fla.

In order to study the effect of nontoxic pigments on the availability of toxic in this vehicle, china clay was added in graded amounts. The volume fraction occupied by the toxic pigment was kept constant in all of the paints at 0.30. This is in contrast to the previously described experiment where the weight proportion was kept constant with a resulting increase in toxic volume fractions. The results of this experiment are presented in Table III. The paint containing cuprous oxide at a volume fraction of 0.30 gave inadequate leaching rates (Table II), and the substitution of as much as 23% nontoxic pigment for an equal volume of matrix did not improve this formulation. The substitution of nontoxic pigments for part of the matrix of the metallic copper paints, likewise, had no substantial effect on the leaching rate. For this vehicle, as well as for Vinylite paints, the leaching rates are related to the toxic volume fraction, and are not increased, at constant toxic volume, by the addition of nontoxic pigments.

The same toxic volume fraction is obtained with a lower weight percentage of toxic in those paints containing the nontoxic pigment. Thus, for cuprous oxide, the paint containing 23.3% inert pigment by weight required only 58.7% cuprous oxide to give the same relative toxic volume, leaching rates, and fouling effectiveness as the paint containing 70% by weight of toxic and no inert. Similarly, 67% metallic copper, when combined with 19% nontoxic pigment, was found equivalent to 77% metallic copper when used alone. Within limits, therefore, a nontoxic pigment may be substituted for an equal volume of matrix without detriment to the antifouling effectiveness of the formulation. This reduces the weight fraction of toxic pigment required in the dry film.

SOLUBLE MATRIX PAINTS

The effect of nontoxic pigments in paints formulated with a soluble matrix (*6*) was studied by the addition of diatomaceous silica to modifications of Navy Specification 52-P-61 formulation. The matrix of this paint consists of 64% rosin, 32% Hercolyn,

and 4% Pliolite by weight. Three series were made in which the total pigment volume fractions were 0.12, 0.18, and 0.24. In each series the total pigment volume was obtained using various proportions of cuprous oxide and Celite. The average leaching rates between the second and sixth months of exposure, and the fouling resistance and physical condition of the paint film after seven months of exposure are plotted in Figure 2 against the volume fraction of cuprous oxide.

The leaching rates of the paints were related to the volume of cuprous oxide, as would be expected, but in contrast to the behavior of the insoluble matrix paints, they did not depend upon the toxic volume fraction alone. They were greater for the paints with the higher total pigment volume when compared on equivalent cuprous oxide volumes.

On the basis of the simplified theory of the action of these paints presented previously (*6*), the rate of loss of cuprous oxide should be related to the paint composition as follows:

$$L_1 = R_2 \frac{w_1 v_2}{w_2}$$

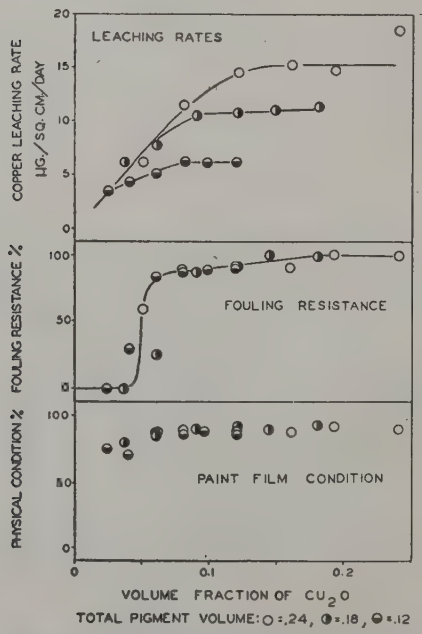

Figure 2. Leaching Rates, Fouling Resistance, and Paint Film Condition Plotted against Volume Fraction of Cuprous Oxide in Paint

Paints contain various proportions of cuprous oxide and of Celite in a matrix consisting of rosin, Hercolyn, and Pliolite

Table IV. Composition, Leaching Rates, and Calculated Matrix Solution Rates

(Paints formulated with a matrix of rosin, Hercolyn, and Pliolite containing various proportions of Cu_2O and Celite)

Composition of Paints[a]					Average Leaching Rate, Cu_2O	Calculated Loss of Matrix (R_2)
Volume Fraction			Weight Fraction			
Celite	Cu_2O	Matrix	Cu_2O	Matrix		
0	0.12	0.88	0.44	0.56	6.7	9.8
0.024	0.096	0.88	0.37	0.60	6.5	12.1
0.04	0.08	0.88	0.33	0.62	7.0	14.9
0.06	0.06	0.88	0.26	0.66	5.6	16.2
0.08	0.04	0.88	0.18	0.70	4.8	19.9
0.096	0.024	0.88	0.12	0.73	4.1	14.0
0	0.18	0.82	0.56	0.44	12.7	12.2
0.036	0.144	0.82	0.48	0.48	12.4	15.1
0.06	0.12	0.82	0.43	0.50	12.1	17.1
0.09	0.09	0.82	0.34	0.55	11.8	23.2
0.12	0.06	0.82	0.25	0.59	9.0	25.8
0.144	0.036	0.82	0.16	0.63	7.0	33.6
0	0.24	0.76	0.65	0.35	21.0	14.8
0.048	0.192	0.76	0.56	0.39	16.6	15.2
0.08	0.16	0.76	0.50	0.42	17.1	18.9
0.12	0.12	0.76	0.41	0.45	16.5	23.7
0.16	0.08	0.76	0.30	0.50	13.1	28.6
0.192	0.048	0.76	0.20	0.54	7.0	24.8

[a] Following bulking values were used in computing volume fraction of these paints: Cu_2O 0.0197 gal./lb., Celite 0.060 gal./lb., matrix solids 0.113 gal./lb.

in which L_1 is the rate of loss of cuprous oxide, R_2 the intrinsic rate of solution of the matrix, v_2 the volume fraction occupied by the matrix, and w_1 and w_2 are, respectively, the weight fractions of cuprous oxide and matrix. The value of R_2 calculated from this equation should be the same for all paints, since no changes in matrix composition were made. As shown in Table IV, the calculated values of R_2 tend to increase as the nontoxic pigment or the total pigment volume increases. The simplified theory is, therefore, not adequate to explain these results. Alexander and Benemelis (*1*) report improvement of similar paints by the introduction of inert pigments. They suggest that increased porosity of the film may be responsible for the beneficial effects of the inert pigment. The observed results could also be explained as an effect of surface deposits if they accumulated to a greater extent on the paints which contain the greater amounts of cuprous oxide. These deposits have been shown to depress the copper leaching rate (*4*).

The fouling resistance of the paints was related solely to the volume fraction of cuprous oxide in the paint film, and was independent of the total pigment volume and of the presence or absence of the nontoxic pigment. This result is in contrast to the leaching behavior described above. Four of the paints containing the lowest total pigment volume had fouling resistance ratings of 80% or greater, although their average copper leaching rates were lower than the usual critical value—ranging from 5.0 to 6.4 micrograms of copper per square centimeter per day. There is no apparent reason why these paints should be more effective than other paints with similar leaching rates. The remaining paints showed the expected correlation between leaching rates and fouling resistance.

TABLE V. EFFECT OF SUBSTITUTING PIGMENTS FOR CELITE ON FOULING RESISTANCE AND PHYSICAL CONDITION OF ANTIFOULING PAINT FILM AFTER EXPOSURE

Pigment Used	Fouling Resistance, %	Paint Condition, %
Celite	90	85
Asbestine	93	100
Venetian red	100	90
Indian red	100	89
Zinc oxide	100	88
Barytes	95	90
Pptd. chalk	50	84

The twelve paints which contained cuprous oxide volume fractions of 0.08 or more gave fouling resistance ratings of 89% or better after seven months' exposure at Miami Beach, Fla. This may be considered the critical volume loading for these paints. Nine of these paints contained various amounts of nontoxic pigment; three contained only the toxic pigment.

The physical condition of the paint film showed little relation to the cuprous oxide volume, or to the presence of the nontoxic pigment. There was a slight tendency for the paints containing the lowest total pigment volume to give somewhat poorer results than the others.

The type of nontoxic pigment may be more important than the amount used in a soluble matrix paint. Babel (*2*) has obtained different results depending upon the type of nontoxic pigment used. The effect of substituting various pigments for the Celite in Navy Specification 52-P-61 paint is shown in Table V. All the paints gave satisfactory fouling resistance for six months at Miami Beach, Fla., with the exception of the one containing precipitated chalk. Only three paints, however, were rated better than 90% in both fouling resistance and paint film condition at this time. These three contained asbestine, Venetian red, and barytes as the nontoxic pigment.

DISCUSSION

These experiments show that the presence or absence of a nontoxic pigment in paints made with insoluble matrices has no effect on the antifouling performance provided the proportion, by volume, of the toxic pigment in the dry paint is maintained constant. The results can be explained on the basis of continuous contact of toxic particles. It seems, therefore, unnecessary to postulate that the increase in permeability of these films influences their antifouling effectiveness.

In the design of antifouling paints formulated with an insoluble matrix it is necessary to first determine the toxic volume loading required to give adequate toxic release. For Vinylite, Vinylite-rosin, and short oil varnish vehicles, for example, toxic volume fraction of cuprous oxide required is from 0.3 to 0.35. The total pigment volume loading to give the desired physical properties can then be studied by substituting various amounts of nontoxic pigment for equal volumes of matrix. This leaves the toxic

volume fraction unchanged, so that equivalent antifouling results from all paints of the series may be expected.

In soluble matrix paints, the presence of the nontoxic pigment results in somewhat higher leaching rates at equal toxic volume fractions. The fouling resistance of the paints and their physical performance during exposure in the sea appear to be independent of the presence of nontoxic pigment. Above a certain toxic pigment volume, which may be expected to vary depending on the composition of the matrix, all paints give satisfactory fouling performance regardless of the presence of nontoxic pigments. The authors' experiments indicate that satisfactory results may be obtained with a variety of pigment volumes.

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RECEIVED August 2, 1947. Contribution No. 399 of the Woods Hole Oceanographic Institution. The experiments were conducted under contract with the Bureau of Ships, Navy Department, which has given permission for their publication. The opinions presented here are those of the authors and do not necessarily reflect the official opinion of the Navy Department or the naval service at large.

PRINTED IN U. S. A.

Contribution No. 401

308. A NEW SPECIES OF *NONION* (FORAMINIFERA) FROM THE WOODS HOLE REGION[1]

By W. S. Butcher

Abstract A new species of the foraminiferal genus *Nonion* is described. The habitat of this species is the brackish water of the tidal ponds of Cape Cod, Massachusetts. It is apparently living in the ponds today and is thus a Recent species. The proposed name is *Nonion tisburyensis.*

Introduction

In the course of a geological investigation of the tidal ponds of Cape Cod and nearby islands, the fauna of the sediments was noted. It was recognized that in the surface layers and for an undetermined depth below, a species of *Nonion* was very abundant. In order to identify this species, Cushman's monograph on the Nonionidae (Cushman 1939) was consulted. It was evident to the author that the species found in the ponds was decidedly different from any of those figured by Cushman. The relationship of this foraminifer to the genus *Nonion* is evident from the planispiral perforate calcareous test with the simple aperture at the base of the apertural face (Cushman 1940). The appearance of foraminifera in the brackish pond water and the lack of correspondence with any described species has lead the author to propose the new species *Nonion tisburyensis.* The specific name has been derived from the name of the pond where first found, Tisbury Great Pond, Marthas Vineyard, Massachusetts. It is also found at Great Pond, Falmouth, Massachusetts, and presumably elsewhere in the general area in brackish water. In both localities it inhabits brackish* water which may be frozen during the winter months.

Figures 1-3. *Nonion tisburyensis* Butcher, n. sp. × 60. 1, Holotype. 2, 3, Paratypes. 1, 3, Side views. 2, Apertural view.

[1] Contribution No. 401 from the Woods Hole Oceanographic Institution.

* At the type locality the salinity of the water ranges from 20 to 30. Normal sea water has a salinity of 35.

Description

Nonion tisburyensis n. sp.
Text figures 1-3

Test planispiral, nearly circular in side view, slightly longer than wide; 7-9 chambers in the last formed whorl. Broadly rounded angles. Somewhat involute giving a crescentic apertural face. Umbilicus slightly depressed. Chambers inflated slightly and sutures simple and depressed forming lobate periphery. Some deposition of shell material at umbilicus, but no stellate deposition. Wall smooth, very finely punctate in early chambers, becoming coarser but still fine in later. Aperture a narrow arched slit at base of apertural face. Diameter: 0.64 mm. Thickness: 0.27 mm. Habitat: brackish tidal ponds of Cape Cod, Mass.

The type specimens are deposited at the Cushman Laboratory for Foraminiferal Research, Sharon, Mass. Holotype (Cushman Coll. No. 51893); Paratypes (Nos. 51894-6).

Conclusion

It is clear from the foregoing description and figures than an undescribed species of *Nonion* is here represented. Phleger (personal communication) has not encountered any similar form in samples from the open ocean bottom off Cape Cod and thus this form may be confined entirely to brackish water. It seems worthy of a separate species name from its habitat and differences in form from described species.

This species differs from closely related species particularly in the number of chambers of the test and in their inflated nature. In addition the depressed umbilicus and the lack of shell material deposition at this point are characteristic. Cushman (personal communication) suggests that this species is related to *Nonion pauciloculum* (Cushman 1944) as described from sandy mud in Buzzards Bay, Massachusetts. The latter species has an average of 7 chambers in the adult whorl.

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Contribution No. 402

[From American Journal of Science, Vol. 246, June, 1948, Pp. 329-352]

American Journal of Science

JUNE 1948

ON THE DATE OF THE LAST RISE OF SEA LEVEL IN SOUTHERN NEW ENGLAND, WITH REMARKS ON THE GRASSY ISLAND SITE*

EDWARD S. DEEVEY, JR.

ABSTRACT. Borings and pollen analyses in salt marsh, coastal pond, and inland bog deposits in southern Massachusetts have provided a date for the postglacial rise of sea level which has long been known in this region. The earliest definite date for the rise is late C1, in the Connecticut pollen chronology (just preceding C2, the oak-hickory zone, regarded as the equivalent of the "post-glacial climatic optimum"). At Grassy Island in the Taunton River, where salt marshes overlie archaeologic remains, the recorded sea level rise is shown to have taken place in C3, (the oak-chestnut zone), and some additional evidence is found for the remarkable geomorphic history worked out for this site by Johnson and Raup. But, as is often the case with salt marsh deposits, only a relatively late date is recorded here, and in working backward from C3 advantage has been taken of the fact that inland localities in the Cape Cod district have been caught in a rise of water table. In the Woods Hole region the history of the vegetation since early C2 has been abnormal, and the abnormality is considered to reflect the rising water table. Apart from this inferential evidence definite stratigraphic data (diatoms in the lake deposits) are available from Oyster Pond to show that the fresh-water phase of the pond's existence was brought to a close in C2 by the rising sea level. The significance of the dating is only local at present, but it is expected ultimately to contribute to a solution of the extraordinarily complex geographic problems arising from the glacial and postglacial shoreline changes in eastern North America. Unfortunately the vertical extent of the postglacial drowning cannot be estimated on the basis of such evidence as that presented here.

INTRODUCTION

OF the many sorts of evidence indicating a geologically recent rise of the sea with respect to that of the land from Connecticut northward, information provided by salt marshes is on the whole the best known and the most satisfactory. The usual section of a New England salt marsh, as

* Contribution Number 402 from the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

pointed out by Douglas Johnson (1925), and discussed by many writers (Knight, 1934; Chapman, 1938; Frederick Johnson, 1942; Johnson and Raup, 1947), shows salt-marsh peat, in places as much as 20 feet thick, overlying deposits which may indicate quiet waters in brackish lagoons, but which in critical cases include fresh-water swamp materials and even forests *in situ*. The salt-marsh peat almost invariably is composed throughout of remains of the high-tide plant associations, especially *Spartina patens*, and it is therefore considered that the sea level has risen at a rate essentially identical with the rate of peat formation. This rate is variously estimated, but the most commonly accepted figure is 12 inches per century.

The belief (long known as the Mudge-Davis theory) that New England salt marshes owe their origin and development to a rising sea level has superseded the Shaler theory, which assumes a stable shoreline. As Knight (1934) pointed out, however, even Mudge-Davis marshes must have been preceded by lagoon filling in order to provide a firm substratum for the *Spartina patens* association, and this filling, initiated around the stands of eel grass (Zostera), could have taken place at a time when the sea level was not rising. Knight's section of the marsh at Killam's Point, Branford, Connecticut, showed several layers of deposits laid down below high-tide line, including as fossils *Spartina alterniflora* (= *S. stricta* of Knight and other authors) and the mud snail, *Ilyanassa obsoleta*. Knight argued that these deposits represent the "Shaler" stage of the marsh, and that they have been preserved at Killam's Point because the marsh has been protected by an island from erosion by the advancing Mudge-Davis sea. On this view Shaler marshes are rare because their remains have been either removed by erosion or buried under advancing offshore and baymouth bars as the sea rose over their edges.

It is possible to accept Knight's theoretical views on the origin of New England salt marshes, and his interpretation of the Killam's Point section, and yet to retain some reservations. The marsh is capped by *Spartina patens* (high-tide) peat, which ends at about 2.5 feet below mean *high* water. *S. alterniflora* (a mid-tide grass) occurs as far down as four feet below mean *low* water, while the lower layer, containing mud-snails which live below mean low water, occurs down to six feet below mean low water, below which level the marsh was

not investigated. Thus "there has been a relative rise of sea level of at least two feet since the marsh at this point reached botanical maturity . . . . and at least four feet since the bottom of the lagoon had been locally filled to a level where [*S. alterniflora*] could grow" (p. 174). But a total rise of six feet seems very small, in view of the 20-foot thickness of high-tide peat reported near Boston (D. Johnson, 1925) and the results reported in this paper. Instances of "fictitious coastal subsidence" (due to local causes such as erosion or compaction of peat) are well known, and it appears that the "early Shaler marsh" at Killam's Point is a converse case of "fictitious coastal stability," a transitory phase of lagoon filling at a relatively late stage in the rise of sea level.

It is not an easy matter to investigate the geology of a rising sea level. If the rise is long-continued it is almost inevitable that the evidence (deposits or erosional features) for a former low stand should be removed by the advancing waves. At the very least such evidence will be drowned and not accessible by the usual methods of inspection. Salt-marshes, the stratigraphy of which can be examined by borings, offer important evidence, but for obvious reasons such evidence can never be taken as necessarily recording the whole history of the delevelling; only the latest phases are likely to be preserved. Moreover, most geologists are less likely to be interested in salt marsh stratigraphy for its own sake than in what it can tell us about movements of the sea and of the land ensuing on the retreat of the Pleistocene ice, whether these movements were the consequence of crustal recoil or of eustatic changes in the volume of the sea itself. If crustal movement was concerned in the delevelling, it becomes of the greatest importance to determine the absolute amount of change of level at various localities, in order to infer the nature and direction of crustal tilting. Because of the complexity of the problem and the insufficiency of the evidence, therefore, all that is known about the last rise of sea level in New England is (1) that it has taken place, and (2) that it was a post-glacial event. We do not know (3) how extensive it was, (4) whether it was equally extensive throughout the region, or subject to systematic regional differences which might imply crustal warping. Nor do we know (5) when it began, or (6) when it ended, there being no agreement on whether the rise

is still going on or has stopped within the last few years or centuries.

Points (5) and (6) emphasize the importance of chronologic information. If we cannot readily tell the earliest time at which the sea began to rise against the land, there remains the possibility of determining the earliest *apparent* time at each of many localities, and thus of ultimately synthesizing a regional picture which might include some legitimate extrapolation. The development of a refined chronology for postglacial time, the chronology based on pollen statistics, makes this approach perfectly practicable.

In this paper a small beginning is made toward the disentanglement of the chronologic aspects of this important geographic problem. Pollen-analytic data are presented to establish, for two localities in southern Massachusetts, the earliest apparent date for the rise of sea level. In one of these localities, Grassy Island in the Taunton River, the salt-marsh section includes an archaeologic horizon, and a relatively late date for the drowning is evident. In the other locality, the Woods Hole region on the southern extremity of Cape Cod, the fact that a rise of water table has taken place at inland sites makes it possible to fix a considerably earlier date for the inception of the delevelling.

THE GRASSY ISLAND ARCHAEOLOGIC SITE

The investigation of the salt-marshes on and near Grassy Island, in the estuary of the Taunton River below the town of Taunton, Massachusetts, was made in July 1945, at the invitation of Frederick Johnson and Hugh Raup. A comprehensive paper on the archaeology, botany, morphology, and history of this site has recently been published (Johnson and Raup, 1947). It remains only to report the results of the pollen analysis, and grateful acknowledgement is made to both these colleagues for the opportunity to participate in this coöperative study and for stimulating advice and assistance in the field. A map of the site is given in Fig. 1, which, together with Fig. 2, is reproduced by permission.

The study of the morphology of this site by Johnson and Raup was made with exceptional skill and insight and has brought to light a remarkably complex set of geographic relations. These must be briefly summarized to make the ensuing

account intelligible. The archaeologic material, long known to science through the careful excavations of Delabarre (1925), implies an Indian village of considerable size or long occupation, or both. It is definitely prehistoric, but otherwise

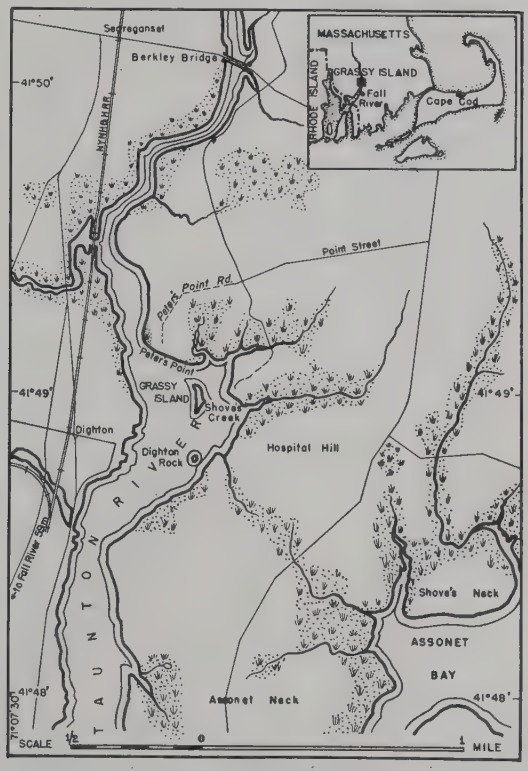

Fig. 1. Map of region in the neighborhood of Grassy Island (from Johnson and Raup, 1947, Fig. 1).

not dateable except in the sense that similar material from other sites in southern New England and New York is commonly regarded as less than a thousand years old. The material lies on till and sand under the present site of Grassy Island, and is covered by a thin layer of black "amorphous peat" of unknown origin, then by a layer of "mixed peat" which, though it contains remains of *Spartina alterniflora*, is

not typical *alterniflora* peat, as it contains masses of *S. patens*. The uppermost layer, 12-24 inches in thickness, is fairly typical *patens* peat. The surface of the island is awash at ordinary high tides, and the archaeologic material lies on a surface which is at least 40 inches below mean high tide. In places this surface is below present mean low tide, and it is clear that such a village could not have been occupied in its present location with sea level at its present position.

The salt-marsh deposits above the cultural remains do not record the steady rise of sea level normally reflected in New England salt-marshes, for instead of a continuous layer of high-tide (*patens*) peat most of the section is made up of mixed peat. Johnson and Raup came to the conclusion that this material is formed by tidal currents sweeping around the island, picking up both high-tide and mid-tide (*alterniflora*) peat on the west side and depositing it in a jumbled mass on the east (or leeward) side. If so, the island may have changed position laterally, migrating in an easterly direction, and a vertical sequence of deposits overlying the archaeologic remains might not record the post-occupational history in the customary way. Examination of the marsh in nearby Shove's Creek (Fig. 1) showed that here again the sediments were anomalous. Near the estuarine edge of the marsh and at other localities in the valley high-tide peat was encountered in a continuous section going down to fresh-water swamp deposits or to the mineral substratum, the maximum thickness being about five feet. Thus the evidence for a rise of sea level of at least this magnitude is clear, and does not depend on the peculiar situation at the island itself. But in the center of the marsh, along the meandering tidal stream, a lenticular mass of mixed peat was found to underlie the *patens* peat, and this deposit is attributed to erosion of mid-tide and high-tide material from the cusps of the meanders and its redeposition in the bights. Lateral and longitudinal shifting of the meanders would account for the uniformity of the deposit, which comes nearly to the surface at the edge of the present stream.

Thus Shove's Creek Marsh does not, as anticipated, provide a standard sequence of salt-marsh deposits which can be used to fill in possible gaps in the Grassy Island sections; for the mixed peat, if its origin is correctly interpreted, could be of almost any age or of several different ages. Evidently salt-

marsh stratigraphy is not a simple matter, and this well-studied example shows how futile it will be in the future to make borings at random in coastal marshes and attempt to elucidate their history on the basis of single sections. The study does, however, offer some confirmation of the hypothesis

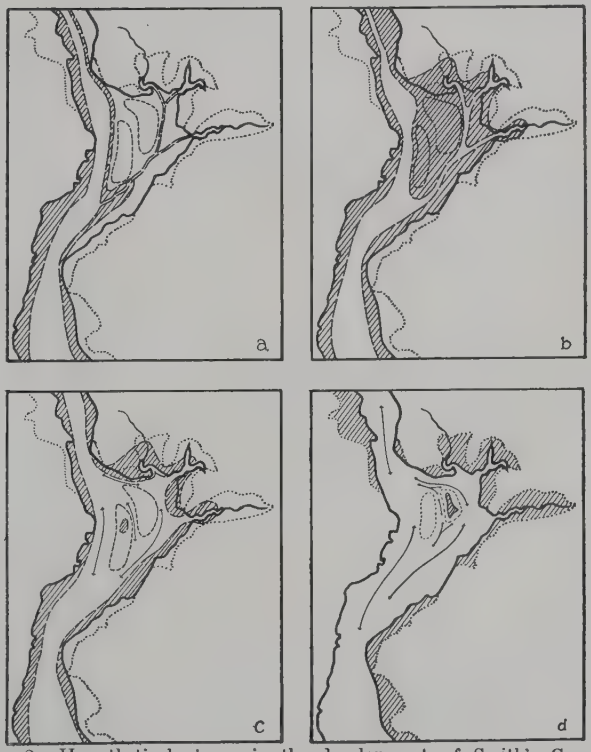

Fig. 2. Hypothetical stages in the development of Smith's Cove and Grassy Island (from Johnson and Raup, 1947, Fig. 8).

of mixed peat formation on Grassy Island itself. If the island is growing toward the east, the high-tide peat should be thicker on the west; reference to the sections show that this is the case, and that the lower surface of the capping layer of high-tide peat is a plane dipping westward with a slope of approximately 10 inches in 200 feet. Projecting this plane westward until it intersects the mineral bottom of the stream, it appears

that the island began its migration at a point about 850 feet west, or at the edge of the deep channel. Measurements made on an apparently reliable map surveyed in 1875 suggest that the island is actually moving eastward at a rate of about 0.7 feet per year: the migration therefore may have required about 600 years.

The history of the Grassy Island region since the beginning of the submergence, as reconstructed by Johnson and Raup, is summarized in Fig. 2. Stage *a* shows the beginning of the rise of sea level in the Grassy Island region, the waters and the marshes not yet having over-ridden the Indian village site. In stage *b* an extensive but shallow marsh is supposed to have covered the whole region, sending arms up the smaller tributaries such as Shove's Creek. This marsh is purely hypothetical, but it is almost inconceivable that the submergence could have taken place without it, and its existence was in fact surmised by Delabarre. In stage *c* continued submergence has increased the velocity and efficacy of tidal scour, and the "Delabarre marsh" has been removed from the center of the estuary, except for a small remnant, the ancestral Grassy Island. The island began its migration, as tidal currents removed its materials from the west side and deposited them on the east, and by stage *d* it had reached its present position. The archaeologic site under the present island is therefore supposed to have been first covered by marsh, then laid bare, and then covered again as Grassy Island moved across it from the west.

So extraordinary a geomorphic history is not easy to prove or disprove by the usual stratigraphic methods, since it implies that sediments have accumulated laterally to a much greater extent than vertically, and a vertical section will not necessarily go through all the pertinent strata. In suggesting that pollen studies be made of the deposits of the region, Johnson and Raup expected that negative evidence would be found, not to support their hypothesis, but to show that it was not impossible. Analyses indicating that all the deposits were of one age within the pollen chronology would constitute such negative evidence. As it happens, however, the pollen studies actually bring forward some positive evidence in favor of their reconstruction.

The pollen diagrams for two borings on Grassy Island itself

and two in Shove's Creek Marsh are presented in Figs. 3 and 4. The analyses proved exceptionally difficult technically, owing to paucity of pollen and the small proportion of grains of forest tree (indicator) species. Several samples were too poor in pollen to justify a count, and in several cases counts of as few as 50 grains had to be accepted, though the counts of all the levels critical for the interpretation are of 100 grains or more.

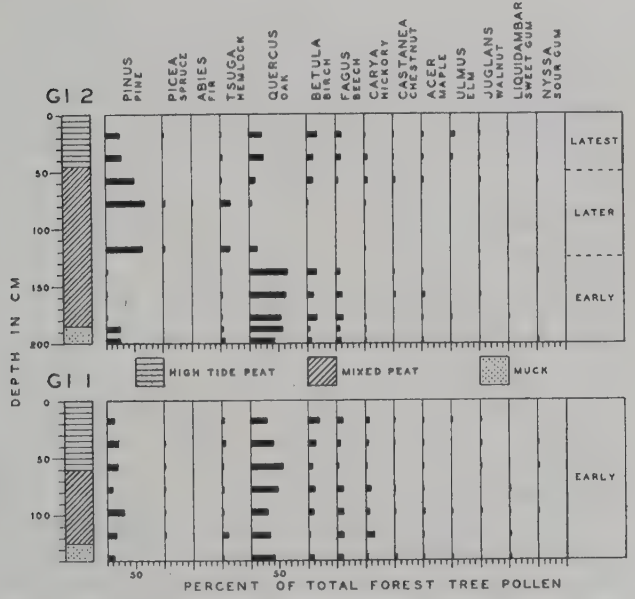

Fig. 3. Pollen diagrams for two borings on Grassy Island. GI 1 is on the western edge of the island, GI 2 near the eastern edge.

It is evident at once that all the borings include material of the latest pollen zone only, i.e. all are C3 in the chronologic scheme for Connecticut (Deevey, 1939, 1943). This was a period of increased moisture compared with the preceding C2, and is characterized in Connecticut as "oak-chestnut." The Connecticut profiles show a suite of changes in the vegetation during the zone: a decline of beech, oak, chestnut, and hickory, and a rise of spruce and pine. All of these changes are visible in Figs. 3 and 4, except that the proportions of chestnut and

of spruce pollen are so small that nothing can be said about their trends. The decline of beech pollen is particularly definite and consistent, despite the small percentages concerned, and as beech pollen is known to have risen across the C2–C3 transition, only to fall again in later C3, the beech curve implies rather definitely that the record of C3 in these profiles is essentially complete.

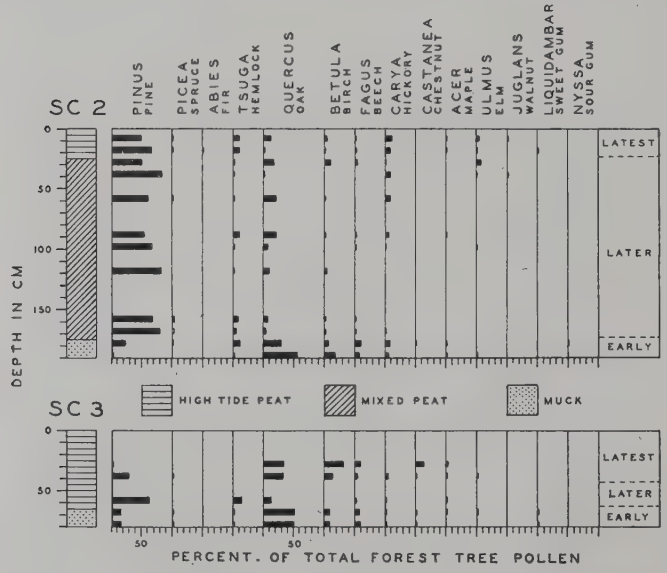

Fig. 4. Pollen diagrams for two borings in Shove's Creek Marsh.

Much more spectacular, however, is the evidence for a threefold division of C3 in this region. It is signalized by the curve for pine pollen, which in borings SC 2 and SC 3 from Shove's Creek and GI 2 from Grassy Island has a more or less strong maximum in the middle part. The gain of pine is made primarily at the expense of oak, beech, birch, and hickory, all of which are a little lower at the level of the pine maximum than above or below. It is not necessary or desirable at present to derive a climatic interpretation for this subdivision of C3. It may well be a purely local phenomenon, recording clearing of the southern Massachusetts forests by the early settlers and

their gradual return toward their original floristic complexity after a pioneer stage of pine dominance. It may be that the changes are strictly confined to the rather sandy terraces in the vicinity of the Taunton River itself. But the changes, whatever their cause or causes, are absolutely consistent in the three profiles mentioned, and their chronologic value is great. For the area in question we can say definitely that C3 saw an "early," a "later," and a "latest" phase.

Looking now at the two borings from Grassy Island, the most reasonable interpretation of their remarkable differences is that GI 1, which is on the west side of the island, is all "early." As the "early" and the "latest" phases are so much alike in respect to their pollen spectra, it is impossible to rule out the alternative explanation that in GI 1 the muck and mixed peat are "early" while the high-tide peat is "latest," the intermediate "later" phase being missing. But on either interpretation the eastern side of the island is younger than the western—if not through the entire section, at least in the mixed peat. A third alternative, that all of GI 1 is "latest," seems to be eliminated by the consideration that pine pollen is too low and oak and hickory are too high.

This evidence is perhaps not quite so critical as it seems. One has constantly to remember that the interpretation of the mixed peat requires lateral accumulation of deposits within a zone whose vertical extent is extremely small. The implication is that sediments and the pollen they contain may have been so completely stirred together that no pollen stratigraphy is permissible. Were it not for this disturbing possibility, one might be tempted to argue that the eastern side of Grassy Island, since it contains the deepest section of "early" material found in the region, has always been approximately where it is, and that only the western edge has migrated. But perhaps the only safe conclusion is that, if pollen analysis means anything at all in this singular context, it means that the western side is older than the eastern, and that the reconstruction of Johnson and Raup is very probably correct.

Apart from the details of the Grassy Island chronology, it is of some importance to be able to say that the drowning of the Indian village began in C3, probably early in that period. This dating does not, of course, provide an estimate in years, and the most that can be said is that the figure arrived at by

Johnson and Raup (600 years ago) is not unreasonable. It fits well with previous estimates of the rate of rise of sea level, and it is checked by the rather slippery evidence provided by the submergence of Dighton Rock just to the south of Grassy Island. While 600 years as an estimate for the total length of C3 seems conservative to the writer, it is good

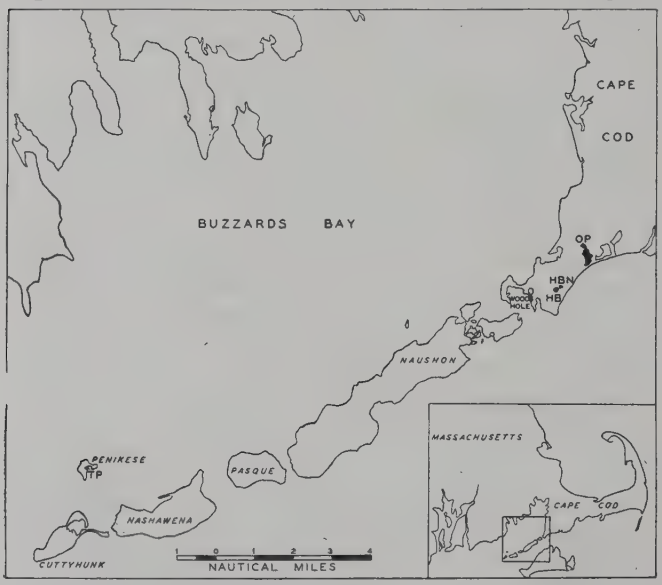

Fig. 5. Map of the Woods Hole region of Cape Cod, showing sites of borings described in the text: OP, Oyster Pond; HB, "H" Bog; HBN, "H" Bog North; TP, Typha Pond.

policy to keep such estimates conservative, and there is of course no positive proof that the whole of C3 is included in the record. The following section will show, however, that the Grassy Island submergence was relatively late, and that evidence of a considerably earlier rise of sea level has been preserved in the Cape Cod district.

SEA LEVEL CHANGES IN THE CAPE COD REGION

Although little is known of the details of the last rise of sea level in the Cape Cod district, the available information is at least not out of harmony with that obtained elsewhere

on the New England coast. Several salt-marshes have been investigated along the Buzzards Bay shore as well as on Martha's Vineyard and Nantucket (D. Johnson, 1925), and at Quisset Harbor, on the Buzzards Bay side of the Woods Hole region now to be considered, Bartlett (1909) has reported a Chamaecyparis (coast white cedar) forest submerged to a depth of perhaps 16 feet by the rising sea level. The new evidence comes from a brackish coastal pond and two Chamaecyparis bogs between Woods Hole and Falmouth, and from Typha Pond on Penikese Island (see map, Fig. 5).

OYSTER POND

The longest boring, the only one to encounter early postglacial sediments, was made in Oyster Pond. This coastal pond, as the map (Fig. 6) suggests, is a kettle, apparently typical of many such ponds in the Mashpee pitted plain which forms the central part of the lower Cape (Mather, Goldthwait, and Thiesmeyer, 1944). As the latter authors have shown, however, the pond heads in Buzzards Bay moraine, which overlies the outwash plain at this locality and elsewhere. When the ice-block melted it let down the moraine as well as the outwash, and the bottom topography of the resulting pond reveals its compound origin. The upper basin, surrounded by moraine, is separated from the lower basin, excavated in outwash, by a sill with a controlling depth of 2.3 meters (the present lake surface standing at about extreme high-water spring tide level). This sill appears to be composed of the original gravel and sand of the late glacial bottom; elsewhere, both to north and to south, postglacial lake deposits have accumulated in the basins, notably in the north basin where 44 feet of deposit were encountered in 15 feet of water at boring OP 2. (It does not follow, however, that the lake in the north basin was originally as deep as 59 feet, and it will be seen that it quite certainly was not). At Boring OP 1 in the south basin a drowned forest was reached by the borer under eight feet of lake deposit at an absolute depth of 19 feet below lake level. The depth of deposit in the center of the south basin was not investigated.

Though doubtless Oyster Pond is ordinarily a fresh-water lake, the high tides and storm waves of the 1944 hurricane washed completely over the basin, and marine debris (Fucus and other seaweeds) still hangs in the bushes to a high-water

mark about four feet above present lake level. In August, 1947, the salinity at the surface was 1.7‰ parts per thousand, and presumably the few large specimens of the barnacle *Balanus improvisus* found living in the lake at that time

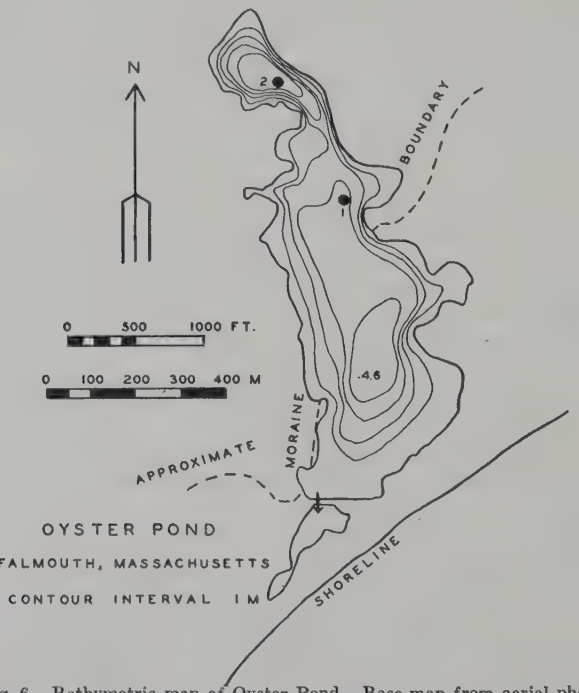

Fig. 6. Bathymetric map of Oyster Pond. Base map from aerial photograph (Fairchild Aerial Surveys, Inc.); sounded 5 August 1947.

developed from larvae carried into the lake in 1944. The rising sea level which drowned the forest at OP 1 may reasonably be supposed to have affected the lake in this intermittent fashion many times in the past when the lake, like the sea, stood at lower levels. But it should be noticed that the marine influence could not have made itself felt in the north basin until relatively late, owing to the presence of the sill, which is in a position to serve as a barrier.

The stratigraphy of boring OP 2, shown at the left of Fig. 7, bears out these considerations. Fresh-water deposits lie at the bottom of the north basin, grading from clay-gyttja

to typical gyttja, and marine influence, as shown by the diatoms, begins at the 19-foot level. (A full report on the microfossils of this section, including animal remains as well as diatoms, is in preparation; critical diatom preparations have been checked by Dr. Ruth Patrick of the Academy of Natural Sciences, Philadelphia). The marine influence continues to the

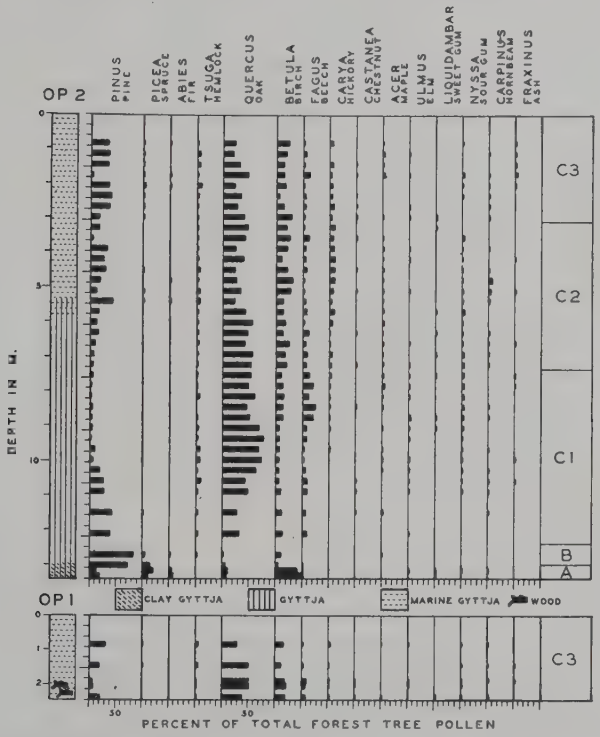

Fig. 7. Pollen diagrams for two borings in Oyster Pond. For location of borings OP 1 and OP 2 see map, Fig. 6.

top, diatoms of both fresh- and salt-water origin being mixed together in the sediments in a way which would be difficult to interpret did we not know the local geography.

The pollen sequence, also shown in Fig. 7, is normal so long as fresh water deposits are being analyzed, the usual pollen zones—A, spruce-fir; B, pine; C1, oak-hemlock—of southern New England being typically represented (Deevey, 1939, 1943). With some difficulty the remainder of the sequence

can also be matched against the Connecticut pollen diagrams: the hickory maximum of C2 is evident, and in C3, although chestnut pollen fails to show its diagnostic rise, the rise of hemlock and the fall of oak, hickory and beech pollen provide a reasonably secure correlation. It is particularly noteworthy that in this locality, at a considerable distance from Connecticut, beech pollen shows the double maximum (at the C1-C2 and the C2-C3 transitions) which was tentatively used in 1943 for a refinement of the chronology established in 1939.

Much more conspicuous in the OP 2 pollen diagram, however, is a series of remarkable departures from the usual sequence in eastern North America. Beginning in early C2, i.e. at about the time regarded as equivalent to the post-glacial "climatic optimum," a series of four almost identical cycles is particularly noticeable in the pine curve. In each of these cycles pine pollen rises rather gradually to a maximum and declines abruptly. In each, with the exception of the most recent, birch pollen takes a reciprocal course, declining to a minimum and rising abruptly. In the last period, birch and pine rise together. In each of the cycles the pine maximum corresponds to a minimum of oak pollen. Grains of other trees are present in numbers too small for their relative strengths to be trustworthy, but there seems to be an incompletely realized tendency for sour gum pollen to reach maxima at pine minima.

At first sight these cycles, which obviously reflect some interruption in the normal development of a climax vegetation in equilibrium with the prevailing climate, might be taken to represent fires. Fire is a potent enemy of Cape Cod forests today, and the tendency of pines, especially *Pinus rigida*, to invade sandy, oxidized soils after fire is well known. It would be extraordinary, however, if the result of a fire were a *gradual* development of a pine forest, followed by a *sudden* resurgence of the more mesophytic oaks and birch. The degree of rapidity of these changes would rather be expected to be reversed, were fire their underlying cause. Moreover, as will be shown below, the same (or some of the same) cycles of vegetation, though local in the sense that they probably did not extend beyond the general Cape Cod region, are found at least as far afield as Penikese Island, ten miles from the Cape and five miles from the nearest mainland. It seems more prob-

able, therefore, that the periodic interruption of the vegetational development was due, not to fire, but to drowning of the forest by a rising water table, and that these cycles tell us, almost as definitely as the Oyster Pond diatom stratigraphy, that the sea level has been rising at least since early C2.

How drowning can lead to a gradual incursion of pine, decidedly not a genus of moist environments, and not so interpreted in the case of the B period, is an interesting question. In general, not only at Oyster Pond, but in the other pollen diagrams presented below, the order of dominance in each of the four cycles is birch-oak-pine, birch-oak-pine, etc. There are exceptions to this generalization, particularly in the other profiles, but probably no more than would be expected in view of the other peculiarities of each profile taken without reference to its neighbors. This sequence then seems to imply, first, an increase in numerical abundance of yellow birch (*Betula lutea*) as the lowlands became moist or actually wet; second, succession toward a somewhat less hydrophytic birch-oak-(sour gum?) forest; third, killing of the lowland forest by continued drowning, so that pine, not necessarily absolutely abundant anywhere except on upland sandy soils, became relatively abundant and contributed a greater proportion of pollen to the lowland sediments; finally, the cycle was repeated, the site of the most important changes perhaps shifting to a new "lowland" as topographic depressions at higher elevations found themselves intersected by a higher water table.

This theoretical explanation doubtless contains a generous measure of special pleading, and is certainly not the only one which could be invented by the practiced botanist. It could not be accepted by itself as proof of a rising sea level. But as we know on quite independent evidence that the sea level has risen during the time in question, the details of the interpretation can perhaps be left to future work. Closer study may in fact reveal whether the rise itself, as well as the rise in water table must have accompanied it, was continuous, as is here assumed as the simplest hypothesis, or was actually intermittent; the latter possibility might facilitate the explanation of the definitely periodic changes in the plant cover. The fact remains that from C2 onward the pollen diagrams of the Woods Hole region are abnormal, and their abnormality itself requires explanation in terms of an advancing shoreline.

THE "H" BOGS

The two Chamaecyparis bogs on property owned by the Marine Biological Laboratory in Woods Hole and located about a mile from Oyster Pond were investigated in September, 1943. Mr. Philip Schafer, whose assistance is gratefully acknowledged, accompanied the writer and gave much botanical

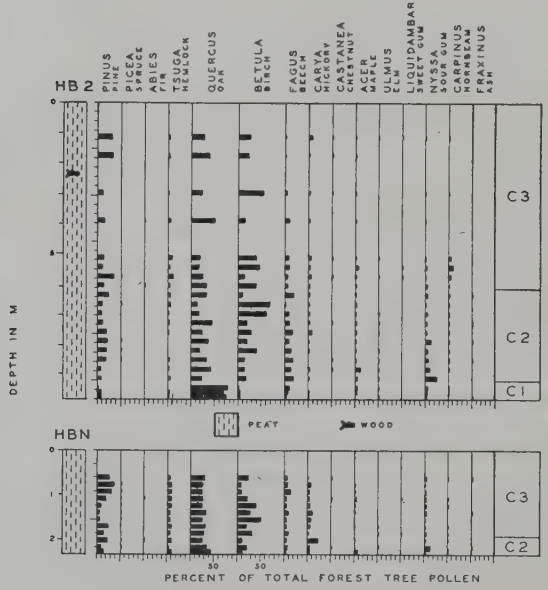

Fig. 8. Pollen diagrams for borings in "H" Bog and "H" Bog North.

information. The larger of the two still has a lake at its center; the smaller, "H" Bog North, is completely covered by a stand of coast white cedar. Islands in both bogs support a sugar maple-beech forest, the understory in the bog forest itself is chiefly a highbush Vaccinium, and near open water at the center of "H" Bog Decodon is the principal mat-former. A drowned forest lies embedded in the floating mat of "H" Bog at depths ranging between five and eight feet, while the total depth of peat in "H" Bog North is about the same (seven and one half

feet). Thus there is clear evidence that a rising water table has affected, and probably permitted the formation of these inland basins in the Buzzards Bay moraine.

The pollen diagrams, presented in Fig. 8, are of interest primarily because they confirm in every essential respect the quadripartite division of the pine curve since C2. Details differ between these diagrams and those from Oyster Pond, and the reciprocal oscillation of birch pollen is not so clear for all the four cycles, but in view of the fact that Chamaecyparis pollen is not preserved it is remarkable that the agreement is so close. "H" Bog obviously had its inception late in C1, as shown by the high proportion of oak pollen at the bottom. The boundary between C2 and C3 is placed between the second and the third pine maximum, largely on the evidence from Oyster Pond that this is where it should fall. The solitary maximum in the hickory curve in "H" Bog North contributes to a difficulty which cannot be resolved without additional profiles. In boring HB 2, the hickory maximum, taken to be the regional maximum diagnostic of C2, was preceded by a maximum of sour gum and is associated with the *first* pine peak. In boring HBN the sour gum-hickory sequence seems to be connected with the *second* pine peak, the first being absent. The Oyster Pond evidence is equivocal, the sour gum curve being devoid of genuine maxima. The question is whether "H" Bog North began its formation early in C2, and thus more nearly synchronously with "H" Bog, or late in C2 as the pine diagram suggests. Further work will probably show that small sour gum peaks are correlated with birch maxima as part of the "hydrophytic-mesophytic-pine" periodic sequence, and that a given profile will show some but not all of these pollen spectra with the same clarity. The fact is that regional climatic shifts from C2 to the present are swamped, in the Woods Hole region at least, by the vegetational peculiarities supposedly related to the drowning, and the present evidence is inadequate for working out this fascinating botanical problem.

In summary, the "H" Bogs confirm and amplify the evidence of a rising sea level. Located at positions well out of reach of the advancing sea, but so situated as to record the rising water table from relatively early times, they push the earliest apparent date for the rise in southern New England back to C1 in the pollen chronology.

TYPHA POND

As part of the Agassiz Diamond Jubilee Expedition to Penikese Island on 3 August, 1947, a boring was made in Typha Pond. This tiny fresh-to-brackish pond, surrounded by Typha with *Spartina patens* near the seaward edge, is now defended from the sea with fair success by a barrier beach. Eight feet of sediment were encountered, the lowest levels apparently a

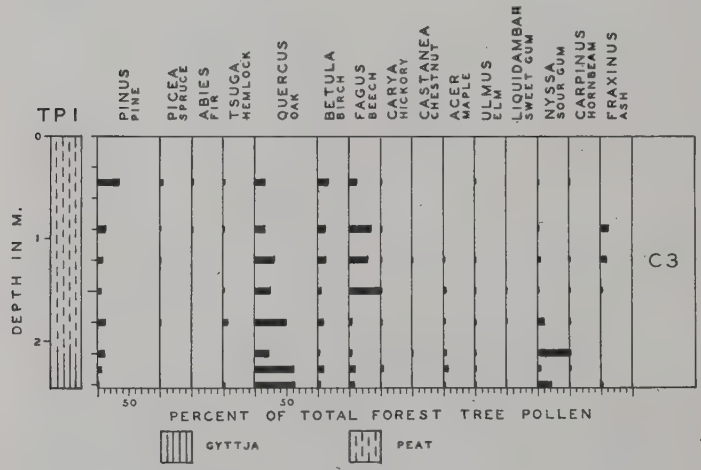

Fig. 9. Pollen diagram for boring in Typha Pond, Penikese Island.

fresh-water gyttja, though no great depth of water is implied by the deposit. Above this is a very silty salt-marsh peat. The pollen diagram (Fig. 9) is not very illuminating. It evidently implies, however, that the pond began to hold water some time in C3, as the water table rose. The phase of deposition seems to include the last two pine peaks of the adjacent mainland, the earlier (taken to be early C3) apparently being masked by the extraordinarily sharp maximum of sour gum pollen. The latter must be a local phenomenon, yet one suspects that it is not unrelated to the four-fold cycle previously discussed. Other local peculiarities, such as the high percentage of beech and ash pollen, are doubtless to be expected. On small islands more or less chance departures from the regional forest composition are likely to be disproportionately represented

in the pollen rain reaching an open site such as a pond or marsh. Typha Pond merely adds one more small piece of evidence that the sea level has been rising in the Cape Cod region, and that water tables have risen concomitantly at sites not too far removed from the coast. But the date provided for the rise is now not the earliest known date, even though it agrees with the one first established in this paper, that from Grassy Island.

CONCLUSIONS

It is clear that the sea level in southern Massachusetts has been rising at least since the latter part of C1 in the pollen chronology. The initial date may have been earlier, for various microfossils from C1 and earlier in the deposits of Oyster Pond, to be discussed in detail in a future communication, imply that the pond was always shallow, and that deposition has kept pace with a rising water level almost since the pond was formed. But accepting late C1 as the earliest secure date, we may inquire where this information fits in with what is already known.

It is unfortunate that the total magnitude of the rise described here cannot be fixed with any confidence. It is rather unexpected to find marine influence at a depth of 19 feet in boring OP 2 (absolute depth below present lake level 34 feet) behind a sill rising to a controlling depth of seven feet. The latter figure is obviously too small as a measure of the rise; but the former is meaningless, since if sea water reached the north basin of Oyster Pond at all it would have left its traces at the bottom of the basin whatever its depth. The presence of wood at an absolute depth of 19 feet in boring OP 1 would be more helpful if we could be sure that the drowned forest is *in situ*. But in any case the pollen diagram shows that the whole of this section is C3. Thus even if the forest were *in situ* only a minimal estimate of the rise would be provided. The fact that 32 feet of peat has accumulated in "H" Bog since its formation late in C1 gives some idea of the total amount of rise. For while this figure is unreliable, being based on a water table rise which was probably not perfectly correlated with the sea level change, it is likely to err on the conservative side.

At Quisset Harbor, just across the moraine from the localities discussed here, Bartlett (1909) has described a submerged Chamaecyparis bog, the bottom of which lies about 16

feet below present high tide level. It was not established that the growth of the bog deposits, which are virtually solid wood, kept pace with a rising water table, though Bartlett believed that it did, and it seems a fair inference in view of the results reported here; it is certain only that at the seaward edge of the bog fresh water peat and stumps *in situ* are now exposed at low tide. But here we have only an assumed magnitude, and no date. At Boston, on the other hand, the Boylston Street Fishweir investigation (F. Johnson, 1942,) has given both a magnitude (16 feet below Boston City Base) and a date (about the time of the climatic optimum (C2 or early C3) for the drowning. It seems, then, that the time relations of the strandline changes were about the same at Boston as farther south, and it may be surmised that the magnitudes were not widely different—but that is the question, and the answer must not be assumed.

On the basis of such fragmentary data we are scarcely in a position to generalize about the character of the post-glacial rise of sea level in eastern North America (see recent summary in Flint, 1947). Investigations of this sort have been carried on in Europe for many years, and workers there are just beginning to be able to disentangle eustatic and crustal bases for delevelling and to use the pollen chronology to establish crustal warping (for the British Isles, see summary in Godwin, 1943). But it is obvious that we cannot carry information directly across the Atlantic from northern Europe to New England. In Finland, Scandinavia and the British Isles it is plain that the big eustatic *rise* of sea level was attendant upon the melting of the ice, and crustal rebound, which by itself should have resulted in a *fall* of sea level, came, or at least was continued, later. In northern Europe and northern North America, north of a line running some 20 miles south of Boston, crustal recoil is the dominant process today (Gutenberg, 1941) and the sea level is falling. But in southern New England at least the latest movement of the sea level is a *rise*.

How these facts are to be harmonized we do not yet know. Theoretical considerations, supported particularly by evidence from the Pacific basin, suggest that eustatic changes since the climatic optimum should have resulted in a world-wide fall of sea level, but even if this proves to be the case, it will hardly help to explain the rise along the coast of southern

New England. It has been argued (F. Johnson, 1942) that the rise is not eustatic, but crustal, being the result of the subsidence of a belt of land peripheral to the ice sheets which was super-elevated in late glacial time by plastic outflow of material at some depth under a crust overloaded and basined by the ice sheet (Daly, 1920, 1934). Marginal super-elevation has been discussed by numerous writers, but no concrete evidence of it has yet come to light. Certainly it is simpler, though not necessarily nearer the truth, to assume that New England south of the zero isobase for recent uplift represents the drowned seaward portion of a late glacial land surface tilted upward toward the north (Antevs, 1928a, 1928b; Hörner, 1929), and that most of the evidence of drowning in pre-C1 times is now submerged at progressively greater depths beyond the present shoreline. The puzzling fact that the rise of sea level has been continued until such a late date along this coast may be due simply to the decantation of Hudson's Bay and adjacent waters whose floors are still undergoing upheaval.

The ultimate solution of this fascinating problem cannot be left to geologic methods alone. Archaeology, ecology, and oceanography are all equally concerned in it. Of the several contributions of ecology, the one which is most desperately needed is a better post-glacial chronology. This is the goal which many ecologists are now actively seeking.

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Contribution No. 403

Reprinted from Ecology, Vol. 29, No. 2, April, 1948
Printed in U. S. A.

THE ABNORMAL DEVELOPMENT OF TUNICATES ATTACHED TO GLASS SURFACES ADJACENT TO ANTIFOULING PAINTS *

Introduction. In an investigation on the comparative tolerance of fouling organisms to copper and mercury when employed as toxic materials in antifouling paints, Weiss ('47) observed that tunicates were particularly sensitive to these materials and were seldom found attaching directly to an antifouling paint. The position of the tunicates in the scale of comparative tolerance was determined principally by their attachment to nontoxic surfaces adjacent to antifouling paints. These adjacent surfaces are protected to varying degree from fouling by the toxics diffusing from the antifouling paint (Edmondson, '44; Harris and Forbes, '46; Miller, 46). In this paper, observations on the abnormal development of tunicates attached to nontoxic surfaces adjacent to antifouling paints are reported. This investigation was conducted at Biscayne Bay, Miami Beach, Florida.

Methods. Microscope slides were painted lengthwise with a band of antifouling paint 10 mm. wide, leaving a clear glass surface 16 mm. wide adjacent to the paint. These painted slides and unpainted ones were immersed in the sea and examined at daily intervals for the attachment and growth of tunicate larvae.

Results. At the period of this study, larvae of the tunicate *Symplegma viride* were attaching daily and in considerable numbers and will be considered the species illustrated in figures 1 and 2. The normal development of *Symplegma viride* attached to an unpainted microscope slide is shown in figure 1. In the

* Contribution No. 403, Woods Hole Oceanographic Institution.

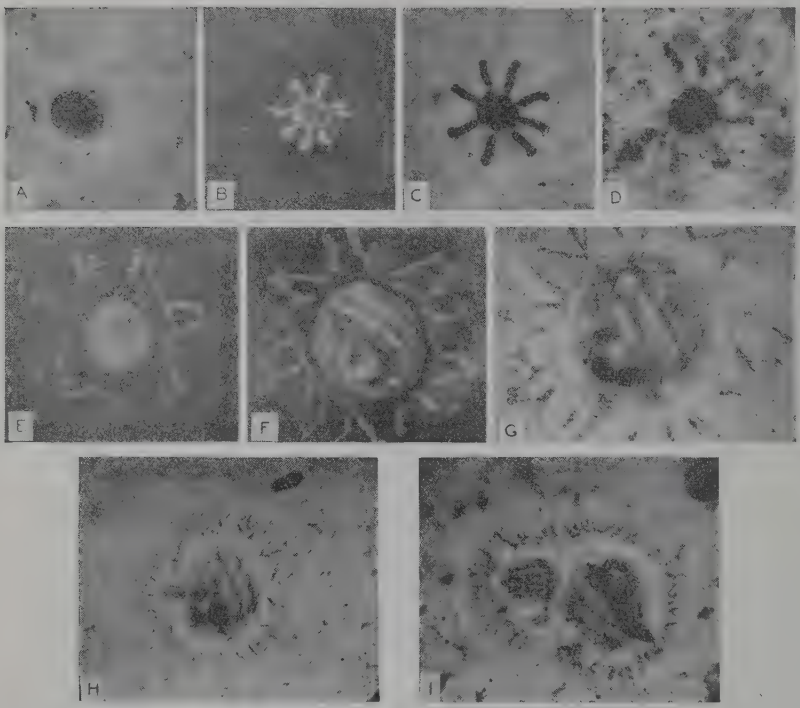

FIG. 1. The normal metamorphosis and development of the tunicate *Symplegma viride*. A, Tadpole larvae just after attaching. B, C, D, less than 24 hours after metamorphosis. E, 24 hours. F, 48 hours. G, 72 hours. H, 4 days. I, 5 days.

normal growth of this species, the extension and symmetry of the peripheral canals is particularly evident. Within a few hours following attachment of the tadpole larvae, eight radiating processes developed from the central bud. Within 24 hours, these radiating canals have been joined together by a system of peripheral canals, all forming part of the circulatory system of the tunicate. By 48 hours, the internal structure of the organism is clarifying with the oral and anal openings and endostyle being particularly evident. After 72 hours, a new bud of the colony has developed within the system of peripheral canals, and by the fifth day following attachment the new colony is developing rapidly with new individuals or buds in addition to the original organism.

As shown in figure 2, in contrast to the rapid expanding growth of the normal developing tunicate, those specimens which had attached adjacent to antifouling paints demonstrated considerable abnormality in their development. The rate of growth was slowed and actually never reached the 24-hour stage of the normal specimens. The connecting peripheral canals never developed and, in addition, the radial canals were characterized by being stunted and by lacking the symmetry of the normally developing tunicate.

The abnormal tunicate growth was demonstrable as far as 10 mm. from the paint edge. Since the attachment and growth of these organisms had taken place on the glass surface, the inhibited and abnormal development must be a result of poisoning by the toxic materials diffusing from the antifouling paints near by.

Summary. Inhibited and abnormal growth of the tunicate *Symplegma viride* was demonstrated on glass surfaces adjacent to antifouling paints.

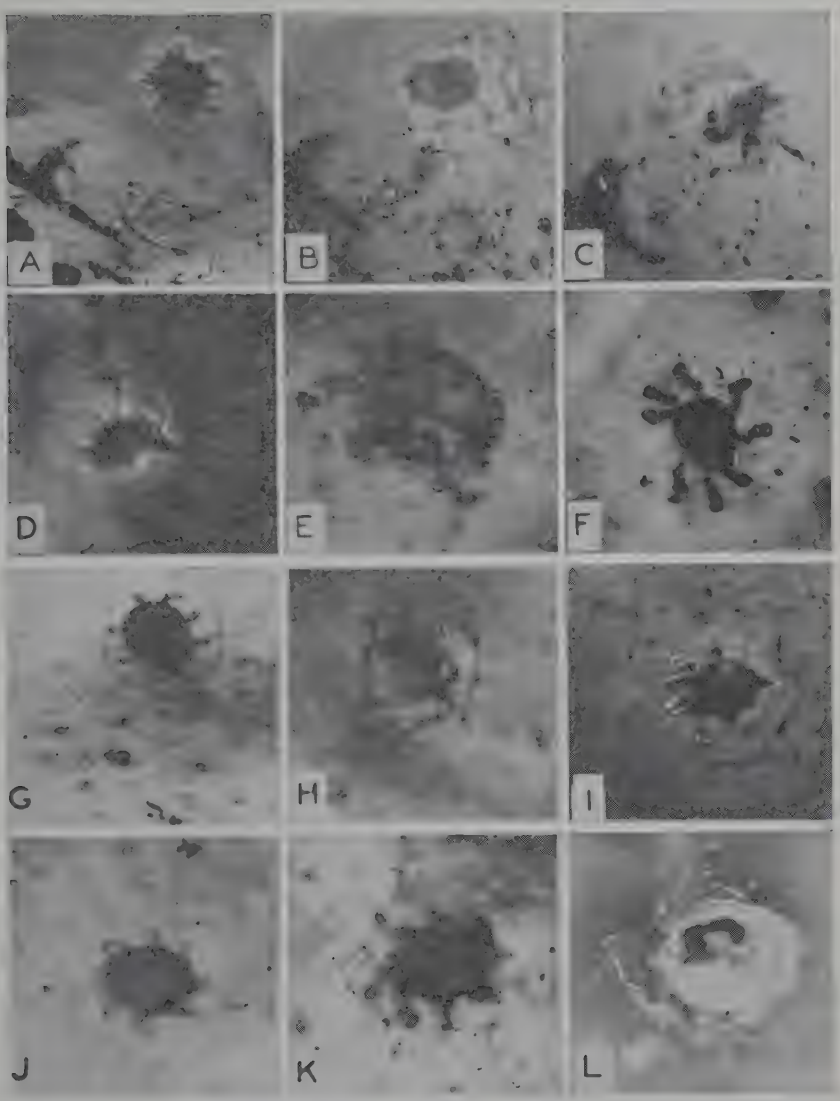

FIG. 2. The development of *Symplegma viride* attached adjacent to and at various distances from the edge of antifouling paints. Each photograph is identified as follows: Antifouling paint, distance from edge of paint and duration of time after attachment. Murcop, 1 mm.: A, 24 hours; B, 48 hours; C, 72 hours. Murcop, 3 mm.: D, 48 hours; E, 72 hours. Murcop, 5 mm.: F, 24 hours. Marblehead Green, 1 mm.: G, 24 hours; H, 3 mm., 48 hours; I, 10 mm., 48 hours. New Jersey Bronze, 3 mm.: J, 24 hours; K, 48 hours; L, 72 hours.

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Contribution No. 404

Reprinted from Ecology, Vol. 29, No. 2, April, 1948
Printed in U. S. A.

THE SEASONAL OCCURRENCE OF SEDENTARY MARINE ORGANISMS IN BISCAYNE BAY, FLORIDA[1]

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Introduction

This paper describes the occurrence and seasonal fluctuations of some of the sedentary marine organisms of Biscayne Bay, Florida, as noted over a period of four years. The species described are those sessile forms recorded from standardized surfaces immersed regularly for one-month periods.

Earlier studies of the attachment and seasonal fluctuation of sedentary marine organisms have been listed by McDougall ('43). Additional papers are those of Edmondson ('44) on the fouling in Pearl Harbor, Hawaii; Richards and Clapp ('44) on the fouling at Ponce de Leon Tidal Inlet, Daytona Beach, Florida; Graham and Gay ('45) on the sendentary marine forms at Oakland, California; and Fuller ('46) on the attachment and growth of such organisms at Lamoine, Maine.

Description of Exposure Sites

Biscayne Bay is separated from the Atlantic Ocean by the islands comprising Miami Beach and the small keys and shoals extending southward (fig. 1). The bay extends north and south for about 32 miles and varies in width from 2½ miles in the widest part of the north bay to about 7 miles in the south bay. At mean low water, the depth of the bay ranges from one foot over the tidal flats to 15 feet in the deeper channels. The tide range is normally about 3 feet. The north and south bays are separated by the causeways connecting Miami and Miami Beach. The southernmost of the three causeways offers an effective barrier to the circulation of water since it is a continuous land fill except for bridges at its eastern and western ends. The other causeways have open bridges between their islands and offer little resistance to circulation. The waters of the north bay are subject to modification by considerable land and sewage drainage. Built-up areas occupy almost the entire shore line. The shores of the south bay, in contrast, have been developed only along the west side between Miami and a point about a mile north of Tahiti Beach.

Three locations were studied. The first one occupied was at Tahiti Beach where the Subtropical Testing Service maintains its racks (fig. 2). This site is 6 miles from the open ocean. The water ranges in depth at the seaward end of the racks from 4 feet at low water to 6 or 7 feet at high water. Records of fouling were kept at Tahiti Beach from September 1942 to June 1944, and again from June to September 1945.

The second exposure site was in the north bay area at the pier of the Beach Boat Slips Corporation, Miami Beach. This site was occupied from September 1942 to May 1946. Test panels were exposed in a covered slip at the outer end of the pier at a distance of 250 feet from shore where the depth is 10 feet at low water (fig. 3). This location is eight miles northeast of Tahiti Beach.

[1] Contribution No. 404, Woods Hole Oceanographic Institution. The present observations were made in the course of work done by the Woods Hole Oceanographic Institution under a contract with the Bureau of Ships, Navy Department. Laboratory space and facilities were provided through the courtesy of the University of Miami Marine Laboratory. To Dr. Charles M. Pomerat acknowledgment is due for the stimulus to initiate this study and for assistance in arranging for several of the identifications. To Mr. Alexander C. Frue and Mrs. Helen S. Magee grateful acknowledgment is due for assistance in checking the counts of many monthly collections.

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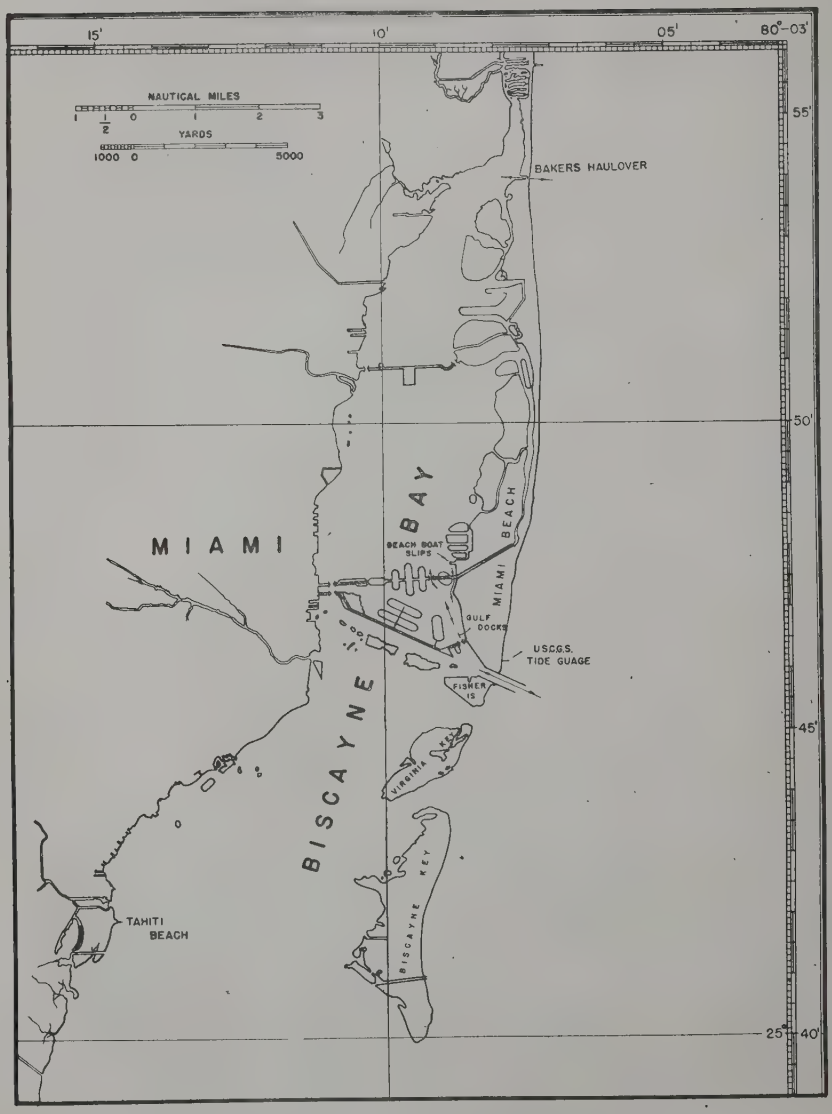

FIG. 1. Map of Biscayne Bay, Florida, showing collecting sites.

The third exposure site was at the Gulf Docks, Miami Beach (fig. 4). Exposures were made from an uncovered pier at a distance of 150 feet from shore. This site is also in the north bay and is located 2600 yards south of the Beach Boat Slips on the same tidal channel. It is 1800 yards from the open ocean.

Records of fouling were obtained at this location from February to October 1945.

During the period of study, daily temperature and salinity observations of the bay water were made at the Beach Boat Slips. Daily temperature and salinity records of the ocean water were obtained from the U. S. Coast and Geodetic Survey Tide Gauge Station located on a pier 450 yards north of the main ship channel. Daily temperature and rainfall records were obtained from the Miami office of the U. S. Weather Bureau. These data have been averaged, or in the case of rainfall totaled, on a monthly basis and are summarized in figure 5.

The waters in the north bay respond quickly and directly to seasonal temperature changes of the air. The inshore ocean waters also show a similar change in temperature. The isolation of the north bay water from the open sea is demonstrated by its salinity which fluctuates much more than the ocean water under the influence of seasonal variation in rainfall. Each year a marked decrease in bay salinity occurs with the initiation of the summer rainy season, but no regular marked decrease in the inshore ocean salinity results. A significant effect on the salinity of the bay water is also contributed by evaporation. During periods of little rainfall, the bay salinity exceeds that of the ocean. This relationship was particularly evident in the spring of 1945.

The circulation of the water in the north bay is developed principally by the tidal flows through the main ship channel and at Bakers Haulover as indicated by

Fig. 2. Exposure site at Tahiti Beach, Florida.

Fig. 3. Beach Boat Slips, Miami Beach.

FIG. 4. Gulf Docks, Miami Beach.

the arrows in figure 1. At the Beach Boat Slips, the salinity of the water fluctuates regularly during the tidal cycle. At low water, the salinity is minimal, having values characteristic of the bay water. At high water, the salinity is maximal, having values similar to the ocean water. The magnitude of this fluctuation varies with the season, being greatest at the end of the summer rainy season when the bay is most dilute, and least at the end of the dry winter season when bay salinities are highest. These relations are illustrated in figure 6, which shows the salinity of the water at the Beach Boat Slips during complete tidal cycles in March and in October 1943.

It may be concluded from these observations that little mixing occurs between water of the north bay and the ocean at each tidal cycle. Apparently, the bay water is pushed back by the ocean water entering at flood tide, but returns unchanged to its maximal extent with the ebb. At the exposure sites at Miami Beach, strong currents are developed by the tidal streams between the closely spaced islands. These bring to the exposure sites bay water and ocean water, alternately.

In the south bay, in the neighborhood of the Tahiti Beach exposure site, there are no marked tidal currents. The bay water probably expands and contracts in area with the flood and ebb tide along its seaward margin. The inshore water, however, probably does not change in character during the tidal cycle, which results merely in a deepening of the bay water as it is pushed back against the shore. However, since the waters are not as restricted in boundary as those in the north bay, mixing with ocean water probably takes place more rapidly and the characteristics of the south bay water are more like those of the ocean.

COLLECTING METHODS

Ordinary window glass, 8 × 10 inches, provided a nontoxic collecting surface 500 sq. cm. in area. One side of this glass panel was sandblasted and coated with the Navy 15HP hot plastic antifouling paint. The dark red paint gave a backing color for the nontoxic surface and provided a more satisfactory fouling accumulator than clear or ground glass alone (Pomerat and Weiss, '46). The toxic surface was required for other studies of antifouling paints which were simultaneously in progress. No limitation of fouling on the nontoxic surface has been noted as a result of the presence of the antifouling paint.

At each of the three exposure sites, the fouling collectors were hung in the sea in a wood rack suspended just below the low-tide mark. The collecting panels were held in a vertical position by grooved supports at the upper corners and at the

center of the bottom edge, and were otherwise open to water movement. At the Beach Boat Slips, the fouling collectors faced the tidal current at an angle of approximately 30°. At the Gulf Docks, the collectors hung parallel to the tidal current, whereas at Tahiti Beach, with no detectable tidal flow, the orientation relative to the current was indeterminate.

In order to ascertain the seasonal fluctuations in the intensity of attachment, the collectors were exposed every two weeks and allowed to accumulate fouling for one month. The panels were immersed on the first and fifteenth of each month and exposed until the first and fifteenth of the following month respectively.

Fouling was enumerated as follows: The total numbers of such organisms as barnacles on the 500 sq. cm. nontoxic area were counted. Barnacles less than 3 mm. in greatest diameter were not counted unless they were the only barnacles present. References to barnacles smaller than 3 mm. have been noted separately in the figures. Colonial organisms forming discrete groups of individuals, such as erect and encrusting bryozoans, were enumerated as individual

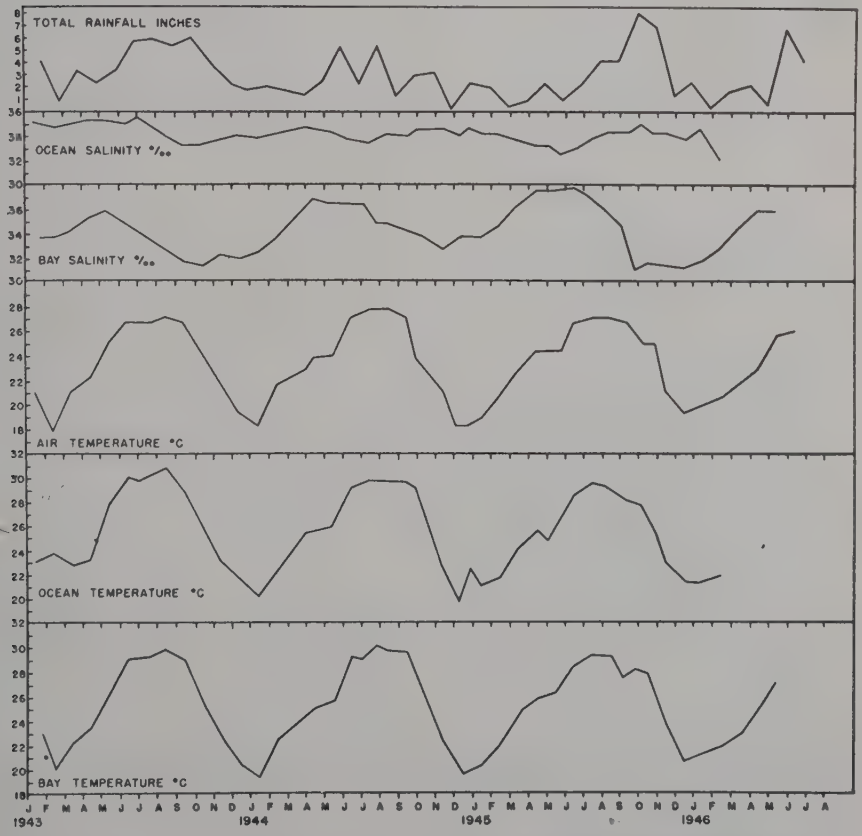
TOTAL RAINFALL INCHES
OCEAN SALINITY ‰
BAY SALINITY ‰
AIR TEMPERATURE °C
OCEAN TEMPERATURE °C
BAY TEMPERATURE °C
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1943
1944
1945
1946

FIG. 5. Monthly averages of daily observations of water and air temperatures and salinity, and monthly totals of rainfall.

colonies. None smaller than 5 mm. in height or diameter was recorded. In the case of colonial forms which spread over large areas, such as hydroids and tunicates, the per cent of the area of the collecting surface covered was recorded. Organisms of sizes smaller than these noted above were designated as incipient fouling. On a nontoxic surface these are the forms which have attached in the last 5–10 days of the exposure period. Organisms successfully attaching at this time are recorded on the fouling collector immersed 15 days later. In addition to the counts, photographs were made of the panels at the end of the period of exposure.

The Fouling Organisms

From the collecting panels and other surfaces exposed for longer periods in the waters of Biscayne Bay, a total of 52 different species of sedentary marine organisms was recorded (table I). Three

Table I. *Fouling organisms recorded in Biscayne Bay, Florida.*

	Beach Boat Slips	Gulf Docks	Tahiti Beach
Cirripedia			
Balanus improvisus Darwin	1	1	1
Balanus amphitrite niveus Darwin	1	1	1
Balanus eburneus Gould	1	1	–
Chthamalus fragilis Darwin	4*	–	4
Tetraclita squamosa floridana Pilsbry	4	4	4
Lepas anatifera Leach	3	1	–
Conchoderma virgatum (Spengler)	–	3	–
Bryozoa			
Bugula neritina (Linnaeus)	1	1	1
Bugula avicularia (Linnaeus)	1	1	1
Watersipora cucullata (Busk)	1	1	–
Schizoporella unicornis (Johnston)	1	1	1
Acanthodesia tenella (Hincks)	2	–	–
Zoobotryon pellucidum Ehrenberg	1	1	–
Tunicata			
Ascidia interrupta Heller	2	–	2
Ascidia nigra (Savigny)	2	–	2
Botrylloides nigrum Herdman	1	1	2
Botryllus planus (Van Name)	1	1	1
Didemnum candidum Savigny	1	1	2
Didemnum candidum lutarium Van Name	1	1	1
Diplosoma macdonaldi Herdman	2	–	2
Ecteinascidia conklini Berrill	2	–	2
Ecteinascidia tortugensis Plough and Jones	2	–	2
Ecteinascidia turbinata Herdman	2	–	2
Eudistoma capsulatum (Van Name)	2	–	2
Microcosmus exasperatus Heller	2	–	2
Polyclinum constellatum Savigny	2	–	2
Styela partita (Stimpson)	2	–	2
Styela plicata (Lesueur)	2	–	2
Symplegma viride Herdman	2	–	2
Annelida			
Hydroides parvus Treadwell	1	1	1
Spirorbis sp.	–	–	1
Dasychone conspersa Ehlers	1	1	1
Coelenterata			
Lytocarpus philippinus (Kirchenpauer)	2	–	–
Obelia oxydentata Stechow	2	–	–
Pennaria tiarella (Ayres)	1	1	2
Plumularia diaphana (Heller)	2	–	–
Obelia dichotoma (Linnaeus)	2	–	–

TABLE I—*Continued*

	Beach Boat Slips	Gulf Docks	Tahiti Beach
Mollusca			
Anomia simplex D'Orbigny	1	1	2
Ostrea virginica Gmelin	1*	–	–
Isognoma alata Gmelin	–	–	4
Pinctada radiata Leach	2	–	–
Algae			
Enteromorpha flexuosa (Wulfen)	–	1	1
Ulva lactuca Linnaeus var. *rigida* (C. Agardh)	–	2	2 & 3
Acetabulum crenulatum (Lamarck)	–	–	2 & 3
Batophora oerstedi J. Agardh var. *occidentalis* (Harvey)	–	–	2 & 3
Callithamnion byssoides Arnott	–	–	2 & 3
Caulerpa verticillata J. Agardh	–	–	2 & 3
Dasya pedicellata (C. Agardh)	–	1	1
Heterosiphonia gibbesii (Harvey)	–	–	2 & 3
Laurencia poitei (Lamouroux)	–	–	2 & 3
Polysiphonia ferulacea Suhr	–	1	2 & 3
Spyridia filamentosa (Wulfen)	–	–	2 & 3

Surfaces and conditions of attachment
(1) Collected on 8 × 10-inch surfaces, one-month exposure.
(2) Period of immersion of collecting surface greater than one month.
(3) Floating surfaces, e.g., rafts and boats.
(4) Attachment to an intertidal surface.
(*) Rare.
(–) Absent or not recorded during period of observation.

of the seven species of barnacles comprised the most abundant organisms both in frequency of occurrence and relative numbers. Next in relative abundance were the erect and encrusting bryozoans respectively, although there were only five species including both types. The Tunicata are represented by more species than any of the other groups, but of the 16 species only three were consistently present on the monthly collectors, the remaining forms developing later in the fouling succession or being too small to be identified at the end of one month of growth.

The other groups of sedentary organisms listed in table I, Annelida, Coelenterata, Mollusca, and Algae, contributed little to the one-month fouling complex at the Beach Boat Slips. The organisms of these groups occurred in relatively small numbers or were limited in attachment by certain ecological factors, some of which are indicated below.[3]

[3] The author wishes to acknowledge the assistance of Dr. Robert H. Williams for the identification of the Algae, Dr. Louis W. Hutchins for the identification of the Bryozoans and Cirripedia, Dr. W. B. Van Name for identification of the Ascidians, Dr. Edward S. Deevey, Jr., for identification of the Coelenterata, Dr. Richard W. Foster for some of the Mollusca identifications and Mr. Harry J. Turner, Jr., for identification of the Annelids.

Cirripedia

Barnacles were the dominant organisms of the fouling on the monthly collectors at the Beach Boat Slips. Separation of the barnacles into the three principal species found on the collectors, from October 1944 to May 1946, showed *Balanus improvisus* to be dominant followed in order by *Balanus amphitrite* and *Balanus eburneus* (fig. 7). From the relative abundance of these three species, it is evident that the fluctuations in the total numbers of barnacles, as shown in figure 8, are due principally to the fluctuations in *Balanus improvisus*.

The marked fluctuations in monthly numbers of barnacles indicate that *Balanus improvisus* is not breeding continuously but is releasing larvae in frequent

pulses. Recognition of distinct seasonal peaks is therefore difficult but in each year a trend was noted toward greater numbers attaching each month, reaching a maximum in the late winter or early spring.

In 1945 the monthly fluctuations in attachment of *Balanus amphitrite* and *Balanus eburneus* were not as marked as for *Balanus improvisus,* but seasonal peaks were more distinct. *Balanus amphitrite* showed three sharp rises followed by a period of slowly decreasing numbers. These peaks occurred in March, May–June, and October (fig. 7). For the period recorded in 1946, the early spring peak was less distinct than the year previous but a definite increase was becoming apparent in May.

The fluctuations in numbers of *Balanus amphitrite* suggest that the settling, growth, and breeding of three yearly classes of this organism may be as follows: The barnacles which settle in March mature and produce the class which attaches in May and June. This class in turn produces larvae which attach in September. The September class does not breed until the following spring. During the winter, when few or no *Balanus amphitrite* attach, the water temperature falls lower than 20° C. which may be below the critical breeding temperature for this species.

The total numbers of *Balanus eburneus* in the barnacle population at the Beach Boat Slips were always small, as shown in figure 7. However, seasonal fluctuation was also apparent with this species. In 1945, the midwinter low of attachment

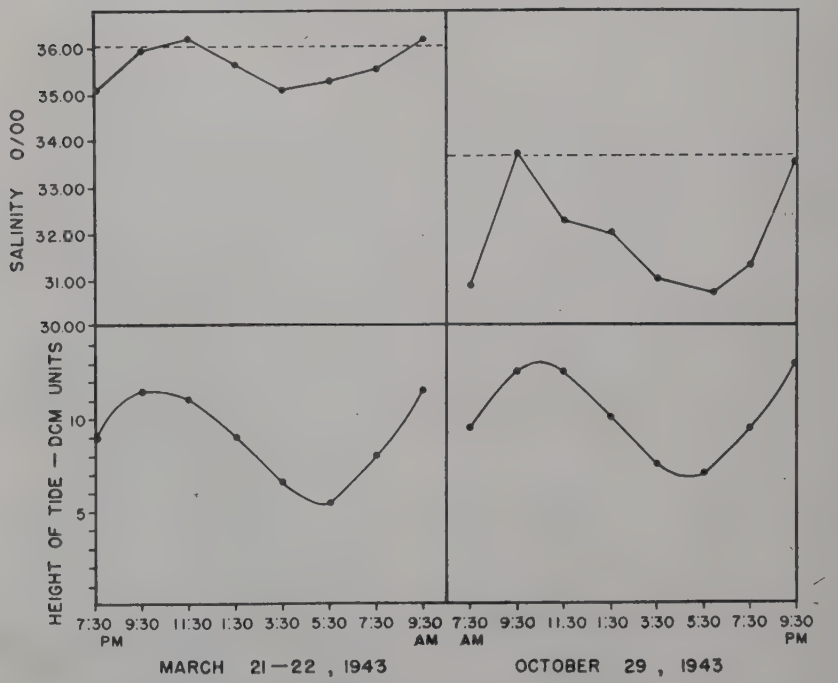

FIG. 6. Relationship between salinity of the water and stage of tide as observed at Beach Boat Slips, Miami Beach, Florida. Dotted line is ocean salinity on same day. Height of tide measured in decimeter units from an arbitrary base line.

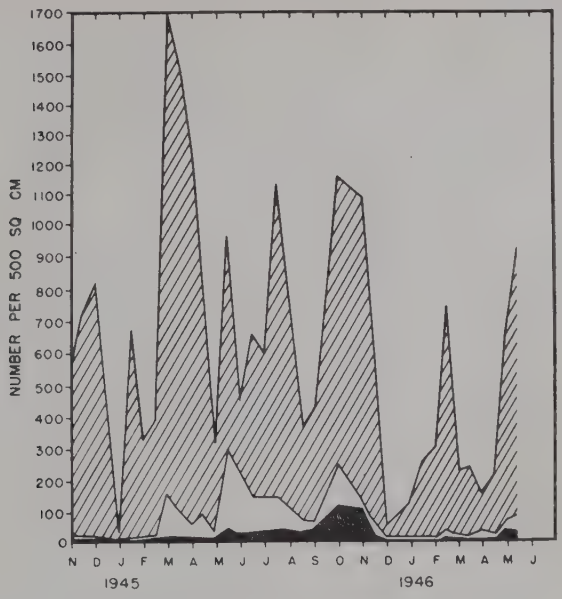

FIG. 7. Monthly attachment of three species of barnacles at the Beach Boat Slips, October 1944–May 1946. Hatched area represents *Balanus improvisus;* white area, *Balanus amphitrite;* and black area, *Balanus eburneus.*

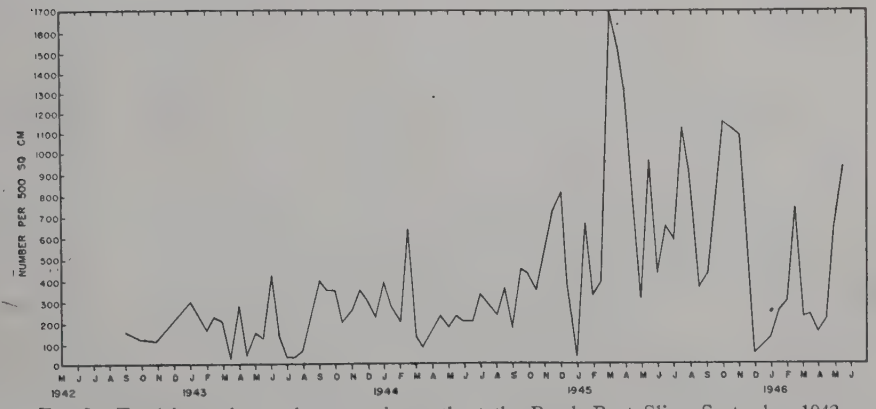

FIG. 8. Total barnacle attachment each month at the Beach Boat Slips, September 1942–May 1946. The numbers are attributable chiefly to *Balanus improvisus.*

was followed by a slow but steady increase, reaching a maximum marked by a peak in October.

Although *Balanus improvisus* is the dominant barnacle of the monthly collections from continuously immersed surfaces, intertidal exposures over a period of six months at the Beach Boat Slips indicated *Balanus amphitrite* to be dominant in the middle and upper zones of the tidal range. As seen in table II, *Balanus amphitrite* comprised only 27.9 per cent of the bar-

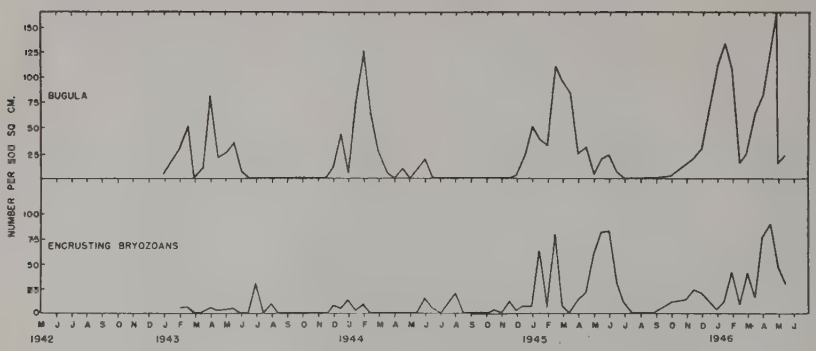
NUMBER PER 100 SQ CM.
BUGULA
ENCRUSTING BRYOZOANS
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1942
1943
1944
1945
1946

FIG. 9. Monthly attachment of erect and encrusting bryozoans at the Beach Boat Slips, September 1942–May 1946.

TABLE II. *Dominance of* Balanus amphitrite *in the intertidal zone as found on 6-inch wood planks exposed October 12, 1944–April 25, 1945*

Distance above low water (inches)	Barnacles total	*Balanus amphitrite*	% of total
>18	16	16	100%
12–18	351	256	72.9
6–12	786	412	52.4
0–6	717	200	27.9

nacle population in the six inches immediately above low water, but was more than 50 per cent of the total population one foot above this point. It was the only species found at the maximum distance reached by barnacles above the low-tide mark. It is also of interest that the maximum numbers of *Balanus amphitrite* attached not in the area immediately above low water but in the second six-inch zone. In the latter zone, the total of other species was also maximal. This distribution may indicate that *Balanus amphitrite* has an optimum zone of attachment above the low-water mark and is able to survive for longer periods out of the water than *Balanus improvisus* or *Balanus eburneus.*

Bryozoa

The encrusting bryozoans, particularly *Watersipora cucullata,* were surpassed only by the barnacles in importance in the fouling population at the Beach Boat Slips. On the monthly collectors, *Watersipora cucullata* and *Acanthodesia tenella*[3] were found in large quantities while *Schizoporella unicornis* was present in small numbers. On long-term exposures, the latter organism usually assumed a dominant role by growing over and smothering barnacles and other fouling organisms.

The two seasonal periods in abundance of these organisms, shown in figure 9, varied from year to year in time and duration as indicated below:

Seasonal duration of encrusting bryozoan attachment

Winter		Dec. '43–Feb. '44	Nov. '44–Mar. '45	Sept. '45–Mar. '46
Summer	June '43–July '43	May '44–Aug. '44	Apr. '45–July '45	Apr. '46—

The summer attachment may be attributed to *Watersipora cucullata,* the winter to *Acanthodesia tenella.*

Two erect bryozoans, *Bugula neritina* and *Bugula avicularia,* were commonly

[3] The identity of this little known species was established by comparison with the types in the British Museum through the courtesy of Dr. Anna B. Hastings.

found. The seasonal fluctuations of these organisms at the Beach Boat Slips are the most marked of all the forms recorded, as seen in figure 9. In each year there are two fairly distinct peaks followed by a smaller rise before the organisms disappear from the collections for several months.

With both species present at overlapping times, the seasonal fluctuations cannot be attributed to one or the other except to the following extent: Both *Bugula neritina* and *Bugula avicularia* were found during the first rise, whereas the second and third of the yearly peaks were due almost completely to *Bugula avicularia*. During all periods of attachment, *Bugula avicularia* was the dominant form.

During the four years in which these organisms were recorded, the disappearance and reappearance of the Bugula was related to the water temperature as indicated in the following tabulation.

Average monthly temperature at disappearance and reappearance of Bugula

	Appeared		Disappeared	
	Month	Av. temp.	Month	Av. temp.
1943	Nov.	22.7° C.	June	29.2° C.
1944	Nov.	22.3	June	29.3
1945	Oct.*–Nov.	28.0–23.9	June	29.5

* Slight rise in attachment.

In the years 1943 and 1944, the reappearance of Bugula took the form of a very sharp increase in numbers, whereas in 1945 a slight rise was first detected in October followed by a sharp increase in November. It is suggested from these data that attachment of *Bugula avicularia* begins when the temperature falls below about 24° C. and ceases at temperatures above 29° C. A very rapid drop in water temperature in October and November 1945 probably accounts for the attachments which occurred during a period when the monthly average temperature was higher than 24° C.

Zoobotryon pellucidum was the only other common bryozoan attached to the monthly collectors. This filamentous form was usually found attached to other forms. Owing to its erratic appearance, *Zoobotryon pellucidum* was not systematically recorded, but it was generally found growing profusely on long-term exposures during the months from May through October, disappearing almost completely during the winter period.

Tunicata

Tunicates occurred on the test surfaces at all times of the year but were present in maximum numbers during the summer months as shown in figure 10. The three tunicates systematically recorded on the monthly collectors were *Didemnum candidum lutarium, Botrylloides nigrum* and *Botryllus planus*. At the Beach Boat Slips, *Didemnum candidum lutarium* attached in each month of the year. Its abundance was maximal in June and July and minimal in September and October. *Botryllus planus* attached during every month except December, January and February and was most abundant during the late summer. The seasonal incidence of *Botrylloides nigrum* paralleled that of *Botryllus planus* but it was absent during a slightly longer period, from November to February.

Other groups

Other groups of fouling organisms were represented in the fouling complex principally by the following species: Annelida, *Hydroides parvus;* Coelenterata, *Pennaria tiarella;* Mollusca, *Anomia simplex;* Algae, *Enteromorpha flexuosa* and *Ulva lactuca*. Of these, *Hydroides parvus* and *Anomia simplex* showed maximal abundance in spring and fall, whereas *Pennaria tiarella* occurred in maximum numbers only in the late summer or early fall (fig. 10). The location of the test collectors under a shed roof at the Beach Boat Slips limited illumination sufficiently to prevent the growth of algae. However, *Enteromorpha flexuosa* and

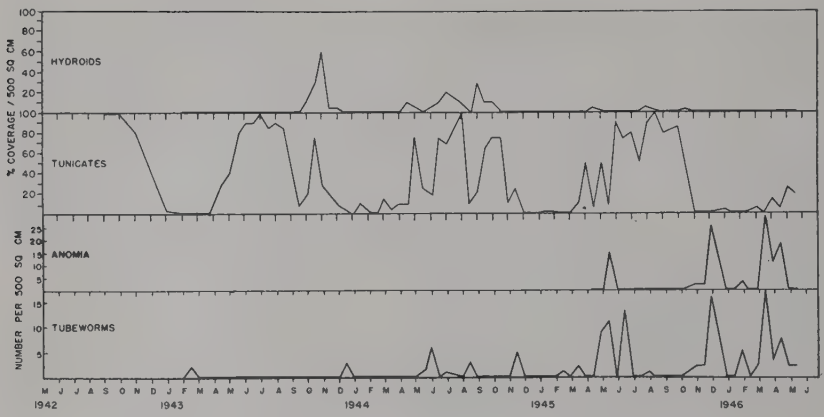
% COVERAGE / 500 SQ CM
HYDROIDS
TUNICATES
NUMBER PER 500 SQ CM
ANOMIA
TUBEWORMS
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1942
1943
1944
1945
1946

FIG. 10. Monthly attachment of hybroids, tunicates, *Anomia* and tubeworms at the Beach Boat Slips, September 1942–May 1946.

Ulva lactuca attached and grew luxuriantly immediately outside the shadow of the shed from February to May but were less abundant during the remainder of the year.

THE FOULING COMPLEX

In the foregoing analysis of the occurrence and season of attachment, each species has been considered individually. However, the various species do not attach on separate panels but complete with each other for attachment and growth space on the same surface. The influence of the various organisms on the attachment and growth of one another is a special problem concerning which some information is provided by the present study.

In the development of a fouling association, several sequences of dominance are evident even in the short-period exposures. The sequences are dependent on the relative numbers of the various larvae in the water at the time of exposure, their tendency to attach, their subsequent rate of growth, and the maximum size attained by the particular species.

The general seasonal sequence of fouling within a year showed marked variation in total fouling in addition to variation from the fouling picture of previous or subsequent years. In figures 11 and 12, photographs of selected monthly collections for the years 1943 and 1945, respectively, serve to illustrate the monthly dominance and the marked seasonal variation. The dominant organisms of these illustrations are listed in table III. In 1943, the spring period was characterized by fairly light barnacle fouling and a gradual increase in the tunicate coverage, which reached a dominant position in the exposure of June 15–July 15. This dominant coverage was replaced by a very rapid increase in barnacle attachments which completely covered the collector in one month of exposure during July and August. Although the numbers of barnacles attaching remained at a high level, their rate of growth in the fall and winter period decreased sufficiently so that they did not cover the collecting surface at the end of the month of exposure during November and December. In contrast, the collections in 1945 showed a dominance shared by barnacles and encrusting bryozoans in the collection of January 15–Feburary 15 which was quickly replaced by the dominance of barnacles lasting until November. An extreme decrease in both numbers of barnacles and

their rate of growth at this time permitted erect and encrusting bryozoans to share with the barnacle the role of dominance.

The organism which most frequently dominates the fouling during the first month of exposure is the barnacle. This is because it frequently attaches in large numbers and its rapid growth quickly covers over the substrate, thus leaving no room for the attachment of others. The colonial forms, such as tunicates and encrusting bryozoans, can attach to and

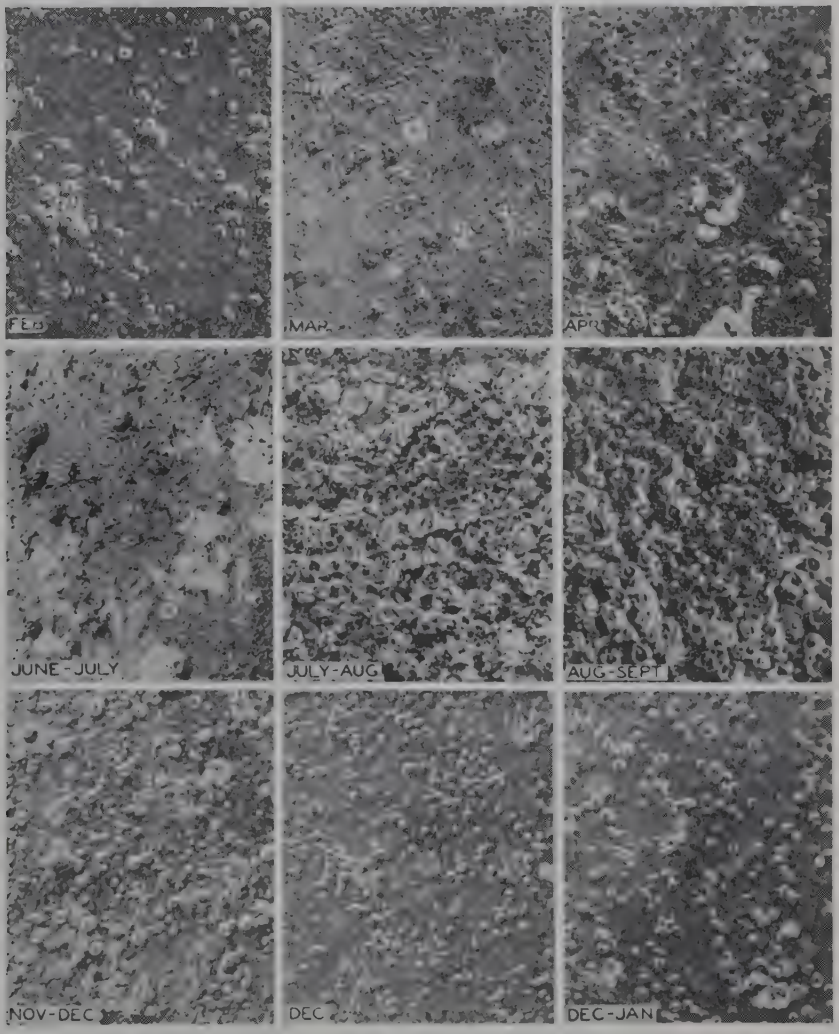

FIG. 11. Selected photographs of the monthly fouling collections at the Beach Boat Slips in 1943. Each photograph represents one fourth of the 500-sq.-cm. collecting surface. The width of each illustration is equal to four inches on the glass collector. Notation of Feb. indicates exposure February 1–March 1, June–July indicates exposure June 15–July 15.

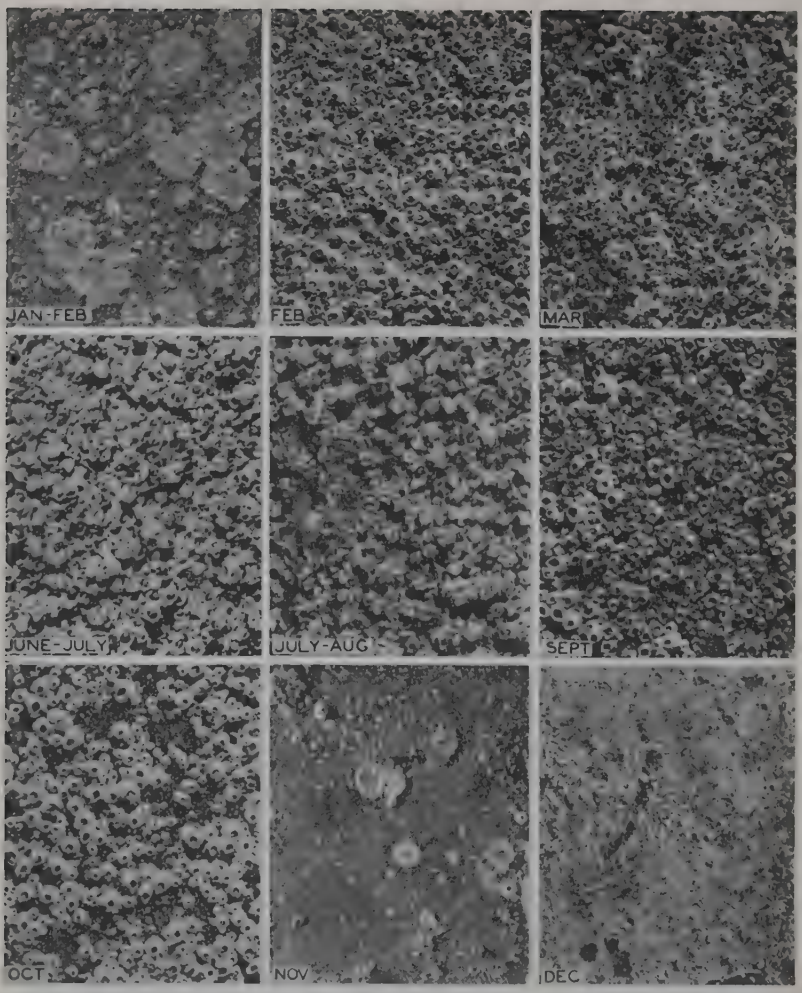

FIG. 12. Selected photographs of the monthly fouling collections at the Beach Boat Slips in 1945. The same scale applies as for figure 11.

spread over other fouling forms and thus limit their growth. The restrictive action of both these organisms is of importance particularly to those forms which grow parallel to a substrate, e.g. tubeworms, or those secondary attachers which fasten to the barnacle. The species which grow vertical to the substrate, such as erect bryozoans and hydroids, are probably least limited by the associated fouling organisms as long as they can secure a satisfactory substrate for attachment.

Although the monthly exposures are usually dominated by the barnacle, this organism in turn can succumb to competition by other organisms in slightly

TABLE III. *Order of dominance of principal organisms on monthly collectors, illustrated in figures 11 and 12*

Month of exposure	1943	1945
January–February		Encrusting Bryozoans Barnacles *Bugulae* Tunicates
February	Barnacles	Barnacles *Bugulae*
March	Barnacles Tunicates *Bugulae*	Barnacles Tunicates Encrusting Bryozoans
April	Barnacles Tunicates	
June–July	Tunicates Barnacles	Barnacles Tunicates
July–August	Barnacles Tunicates	Barnacles Tunicates
August–September	Barnacles Tunicates	
September		Barnacles Tunicates
October		Barnacles
November		Barnacles *Bugulae* Encrusting Bryozoans
November–December	Barnacles Tunicates *Bugulae*	
December	Barnacles Tunicates Encrusting Bryozoans	Barnacles *Bugulae*
December–January	Barnacles Tunicates Encrusting Bryozoans	

Notation of one month, e.g. January, indicates exposure of January 1–February 1.

Notation of two months, e.g. January–February, indicates exposure of January 15–February 15.

longer exposures. In figure 13 a population of barnacles is shown which has been overgrown, after four months' exposure by the tunicate *Didemnum candidum lutarium*. Other organisms attached to the substrate have been effectively smothered or limited. This type of succession is also frequently shown by the encrusting bryozoan *Schizoporella unicornis*, although this species does not spread as rapidly or extensively as *Didemnum*.

In analyzing the barnacle populations, relative to numbers attached and season of the year, there are several factors to be noted as controlling the total monthly collection. These factors are the numbers of barnacle cyprids attaching, the survival of the cyprids, and the rate of growth. It is evident that although large numbers of cyprids may attach, their survival determines the numbers on the monthly collection. Some observations indicate that when cyprids are settling in great numbers survival is poor. A few cyprids attaching daily during the summer when the growth rate is highest can effectively fill the 500-sq.-cm. collector after one month. On the other hand, high daily attachment of cyprids with poor survival and low growth rates may result at the end of one month in comparatively few barnacles larger than 3 mm.

The rate of growth of an organism is of importance in determining its position in an ecological complex, because where many species are competing for a limited area, those growing fastest will tend to dominate the association. The growth rate in turn may depend on temperature.

The relationship of temperature to the first month's growth for the three principal barnacle species is shown in figure 14. For *Balanus improvisus* and *Balanus amphitrite*, the two largest components of the barnacle population, the maximum growth rates are attained at a temperature of about 25° C. At temperatures above this value, the maximum adult size for the species is attained in one month. For *Balanus eburneus*, the growth attained in one month continues to increase with higher temperature, indicating that the maximum or near-maximum size for the species is not attained in this period even at the highest temperature experi-

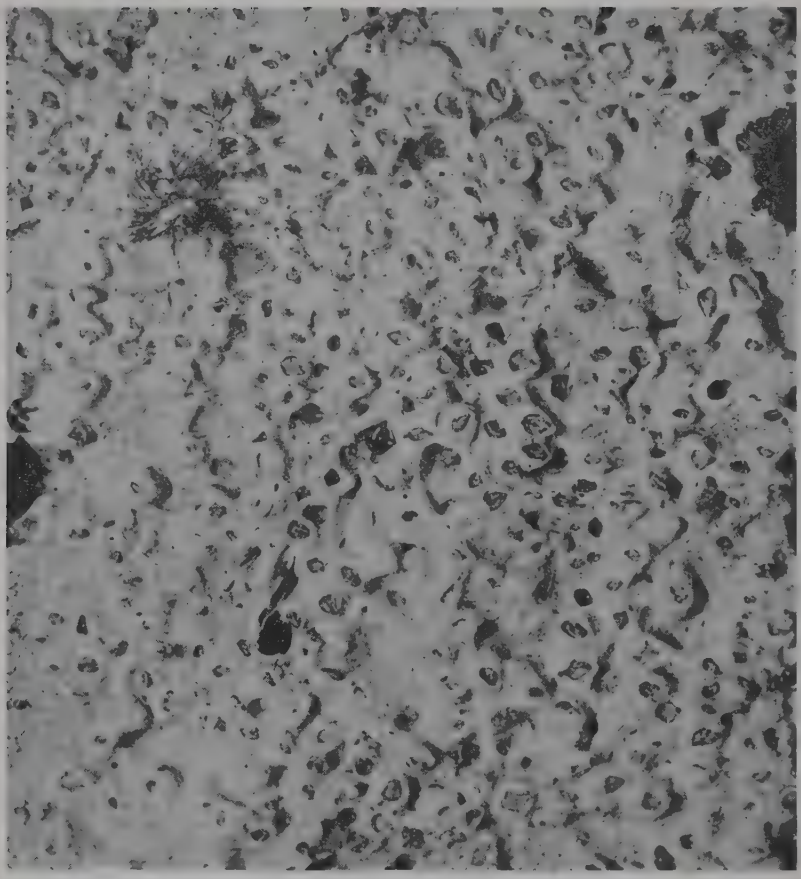

FIG. 13. Fouling complex formerly dominated by barnacles, now overgrown by a spreading tunicate, *Didemnum candidum lutarium*.

enced. The very rapid attainment of large size during the months with temperatures above 25° C. is readily seen as a major factor enabling barnacles to cover collecting surfaces during the summer even though the daily attachment of cyprids in this period may be low.

Comparison of fouling at different locations in Biscayne Bay

Comparison of the fouling records obtained at Tahiti Beach and the Gulf Docks with those of the Beach Boat Slips reveals that, while there is no significant difference in species collected at the three sites and little difference in the period of occurrence, there is great variation in comparative numbers. Figures 15 and 16 illustrate the fouling record at Tahiti Beach and Gulf Docks respectively for the periods in which observations were carried on at these locations. Among the three Biscayne Bay exposure sites, the relative numbers of nearly all of the organisms are greatest by far at the Beach Boat Slips.

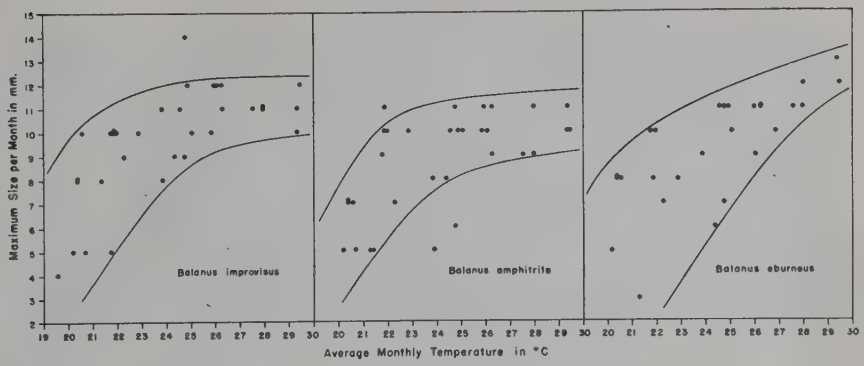

FIG. 14. The relationship between average temperature for any month and maximum barnacle growth observed during that month for *Balanus improvisus, Balanus amphitrite* and *Balanus eburneus.*

In contrast to the Beach Boat Slips worm, *Hydroides parvus,* is dominant where barnacles are the dominant form, during its spring and fall peaks. Al- at Tahiti Beach the calcareous tube- though barnacle cyprids were noted as

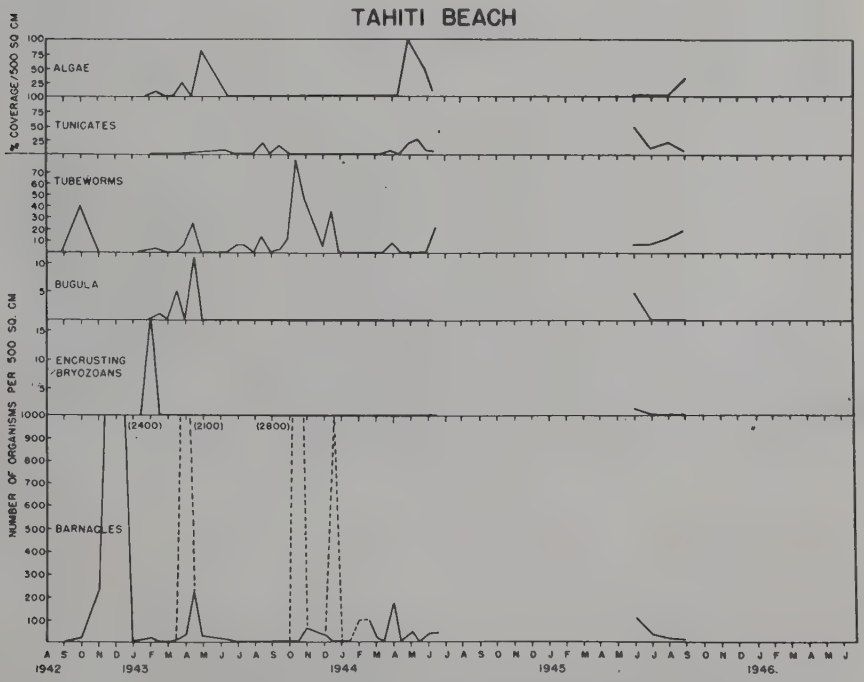

FIG. 15. Monthly attachment of sedentary organisms at Tahiti Beach, September 1942–June 1944 and June 1945–September 1945. Dotted lines represent attachment of barnacles smaller than 3 mm.

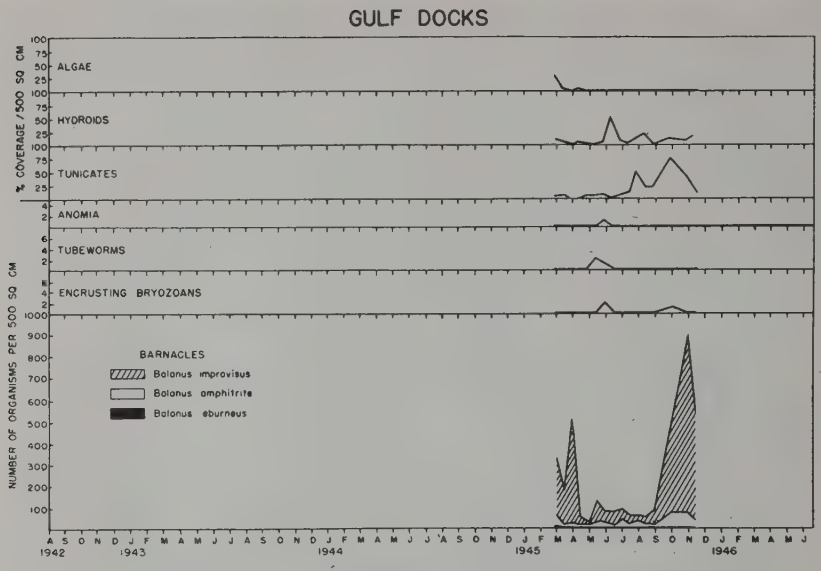

FIG. 16. Monthly attachment of sedentary organisms at Gulf Docks, March 1945–November 1945.

attaching in considerable numbers at Tahiti Beach on several occasions, the production of barnacles larger that 3 mm. was exceedingly limited, due apparently to a combination of high mortality and poor growth rate. The peaks of barnacle attachment at Tahiti Beach are well illustrated in figure 17. The paucity of the monthly collection of barnacles plus the rapid disappearance of the sets was characteristic of this location.

The fouling at the Gulf Docks resembled that of the Beach Boat Slips in species and rate of growth but never attained the numbers which attached at the latter location. The fewer numbers of larvae attaching at the Gulf Docks were most probably due to the proximity of this site to the open ocean, which contributed no significant numbers of fouling organisms on the flood tides. Attachments at the Beach Boat Slips occurred in greatest numbers during the low-tide period when waters from the north bay occupied the exposure site (Weiss, '47).

In addition to the studies at the three exposure locations, several observations were made on the distribution of fouling organisms northward from Tahiti Beach along the west shore of the bay south of the causeways. The fouling along this shore up to the Miami River is characterized by a mixed population principally of barnacles, erect bryozoans and tubeworms, with no particular organism dominating as completely as does the barnacle at the Beach Boat Slips. Between the Miami River and the causeways, the area principally affected by the heavy pollution of the river, algal growth, both *Enteromorpha flexuosa* and *Ulva lactuca*, develops luxuriantly on the water lines of vessels.

Ecological factors influencing fouling

The considerable variation in numbers of individuals and species attaching at the three sites indicates the importance of certain ecological factors. At the Beach Boat Slips, the location of heaviest

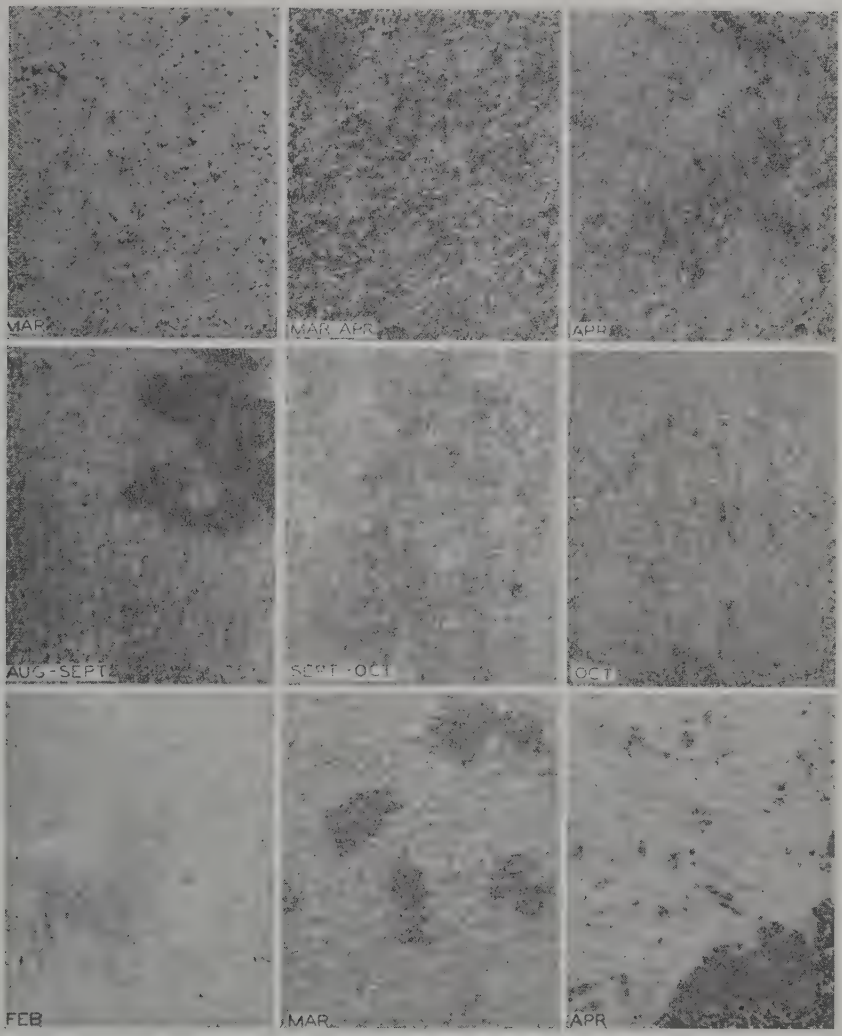

FIG. 17. Selected photographs of the monthly fouling collections at Tahiti Beach, March–April 1943, August–October 1943, February–April 1944. The scale of this figure is the same as described for figure 11.

attachment, the following conditions are found.

1. Periodic exposure on each tide to bay water which is little mixed with ocean water.
2. A body of water surrounded by concrete bulkheads and wharf pilings.
3. Tidal currents reaching maxima of 2–3 knots.
4. Moderately polluted water.

These factors all appear to favor heavy fouling. The lack of mixing and subsequent dilution of the bay water provide for maximum opportunity of the larval

stages of the sedentary organisms to accumulate and attach before being swept to sea. The bulkheads and pilings support fouling communities, which provide and maintain a high density of larvae in free swimming stages ready for attachment. The tidal currents, which maintain a circulation of the water past the sedentary forms, and the pollution may increase the food supply available to the organisms.

The heavy fouling usually encountered in developed harbors, as noted by Visscher ('27), is probably the result of some or all of the factors enumerated above.

At the Gulf Docks these four factors are already considerably modified. For a major portion of the tidal cycle the site is swept by ocean water entering on the flood tide and leaving on the ebb. Only at or near low water does the unmixed water of the bay reach this location with its high concentration of larval stages. Although swept by even stronger tidal currents the non-polluted ocean water may provide a lower nutrient source for the attached forms. The larval stages released from the fouling on the concrete bulkheads near by are probably quickly lost by being swept to sea.

In contrast to these two locations, the conditions at Tahiti Beach do not favor intense fouling. There are no marked tidal currents; the water is little polluted; there is no source of fouling on the surrounding shores, which are occupied chiefly by mangrove swamps. The water brought in by the tide passes over shallow flats, which are not populated by the characteristic fouling species.

Summary

Standardized records of monthly accumulations of fouling organisms were kept for four years at three exposure sites in Biscayne Bay, Florida. Locations surveyed as close together as 2600 yards and as distant as 8 miles showed marked variation in occurrence and intensity of the same fouling organisms.

All the sedentary forms recorded exhibited pronounced seasonal fluctuations in abundance. In addition to seasonal variation several of the organisms demonstrated considerable year-to-year variation in numbers.

The fouling complex in this area tends to be dominated by barnacles in the early succession and by the colonial spreading forms, tunicates and encrusting bryozoans, in the later stages. The ecological factors which contribute to the character and abundance of fouling at the three sites are described.

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Contribution No. 405

Reprinted from JOURNAL OF METEOROLOGY, Vol. 5, No. 6, December, 1948, pp. 265–274
Printed in U. S. A.

VERTICAL EDDY FLUX OF HEAT IN THE ATMOSPHERE

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(Manuscript received 2 January 1948)

ABSTRACT

The thermodynamics of open systems is developed for a special atmospheric system in order to obtain a precise definition of the vertical eddy flux of heat. The upward eddy flux of heat per unit area is $\langle \rho V_z' h \rangle$, where ρ is density, V_z' is a specially defined fluctuation of the vertical component of velocity, and h is specific enthalpy.

In terms of the eddy diffusivity K, the unit-area flux of sensible heat is $-K\bar{\rho}\,\partial \bar{Y}_d/\partial z$, where z is height and $Y_d \equiv c_p T + \phi$ and, in turn, c_p is isobaric specific heat, T is temperature, and ϕ is geopotential. The heat flux including the latent-heat flux due to the flux of water vapor is $-K\bar{\rho}\,\partial \bar{Y}_s/\partial z$, where $Y_s \equiv c_{pd} T_e + \phi$ and, in turn, c_{pd} is the isobaric specific heat of dry air and T_e is equivalent temperature. Other expressions can replace these general expressions under stated conditions.

Under some conditions the rate of loss of heat from the ocean surface by evaporation and conduction to the air, for a given distribution of eddy diffusivity, depends only on the mean surface temperature $\bar{T}_a$ and on the mean wet-bulb temperature $\bar{T}_{wb}$ at a chosen, short distance above. The rate of loss of heat is proportional to the difference in corresponding equivalent temperatures, $\bar{T}_{e_0} - \bar{T}_{e_b}$.

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1. Introduction

The subject of eddy flux of heat in the atmosphere was opened by Taylor in 1914. The upward eddy flux of heat per unit area was expressed as $-k_e\,\partial\bar{\theta}/\partial z$, where k_e is "eddy conductivity," θ is absolute potential temperature, and z is height. His use of this expression (Taylor, 1914, p. 62) was followed by his presentation of its derivation (Taylor, 1915, pp. 2–4). Schmidt (1921) and Brunt (1929, p. 211) have given the correct expression in which the factor $\partial\bar{\theta}/\partial z$ is replaced with $\partial\bar{T}/\partial z + g/c_p$, where T is absolute temperature and g/c_p is the adiabatic lapse rate of temperature.

In spite of the existence of expressions of this type, need is felt for a more satisfactory basis in the formulation of the vertical eddy flux of heat. In the present paper, therefore, this quantity is given a precise edfinition (section 3), which leads to a general expression (section 4), to expressions with the flux of latent heat both excluded (section 5) and included (section 6), and to expressions for the eddy flux of heat from dry ground (section 7) and from large water surfaces (section 8). While some of the expressions have appeared before, all are now placed on a uniform, rigorous basis. In this subject the quantity Y, the sum of specific enthalpy and geopotential, is new (sections 4–8); section 8 leads to a new result of practical importance.

Ertel (1942; summarized by Raethjen, 1944) and subsequently Priestley and Swinbank (1947a; b) have described an important phenomenon affecting the eddy flux of heat: Priestley and Swinbank's (1947b) basic expression for the upward eddy flux of heat per unit area may be written $c_p\bar{\rho}\langle v_z T'\rangle$, where c_p is isobaric specific heat, ρ is density, v_z is instantaneous vertical component of velocity, and T' is instantaneous temperature anomaly. They introduce mixing length l and write

$$T' = -l\left(\frac{\partial\bar{T}}{\partial z} + \frac{g}{c_p}\right) + T''.$$

The eddy is supposed to have last been "at rest" (*i.e.*, $v_z = 0$) at $z - l$, where the eddy had a temperature excess T''. In older theories, beginning with Taylor (1915), it was tacitly assumed that $T'' = 0$. Writing K for $\langle v_z\rangle$, Priestley and Swinbank obtain

$$c_p\bar{\rho}\langle v_z T'\rangle = c_p\bar{\rho}\left[-K\left(\frac{\partial\bar{T}}{\partial z} + \frac{g}{c_p}\right) + \langle v_z T''\rangle\right],$$

where the eddy diffusivity K is "an essentially positive quantity" and the last term is called the "buoyancy term." "Thus if there is any overall tendency, how-

[1] Contribution No. 405.

ever slight, for the warmer eddies to start to rise, the sign of the [buoyancy] term becomes essentially positive and results in a systematic upward flux of heat, irrespective of the sign of $\partial\theta/\partial z$." Because of the buoyancy term, the eddy flux of heat is not necessarily directed downward whenever the lapse rate is less than adiabatic.

Ertel's paper includes the conclusion, apparently untrue (Prandtl, 1944a; b; Raethjen, 1944), that the eddy flux of heat is necessarily directed upward when the lapse rate of temperature is positive.

The mean value of a quantity is indicated throughout the present paper by placing a bar over the quantity or by enclosing the quantity in angular brackets, *e.g.*, $\bar{\theta}$ and $\langle v_z T' \rangle$. Either an instantaneous mean over an area on a level surface or a mean over a time interval at a fixed point is satisfactory in common situations.

2. Eddy diffusivity

If the usual restriction that density experiences no turbulent fluctuation is abandoned, the mean vertical motion needs to be specially defined. The upward component of velocity relative to the earth is represented by v_z. The speed V_z is a weighted mean defined by $\bar{\rho} V_z = \langle \rho v_z \rangle$, and the instantaneous speed V_z' is defined by

$$v_z = V_z + V_z'; \tag{1}$$

hence $\langle \rho V_z' \rangle = 0$. Consequently the upward mass flux across unit area of a motionless horizontal surface has the instantaneous value ρv_z and the mean value $\bar{\rho} V_z$, and the upward mass flux across unit area of a horizontal surface moving upward with the speed V_z has the instantaneous value $\rho V_z'$ and the mean value zero. In other words, V_z is the upward speed of a steadily moving horizontal surface through which there is no net mass transfer.

Treatments of the eddy flux of heat by Taylor (1915), Schmidt (1917; 1925), Brunt (1929; 1939), Lettau (1939), and Priestley and Swinbank (1947b) involve the concept of a length now usually called 'mixing length' ("Mischungsweg," Prandtl, 1926; "mixing length," Prandtl, 1929). This concept requires assumptions regarding the nature of eddies, for instance, that an eddy remains unchanged in properties during displacement from level of 'origin' to the level under consideration, and that the mean vertical distributions of properties are essentially linear between these two levels. For present purposes it is preferable to define eddy diffusivity without reference to mixing length and thus to follow the more direct type of approach used by Richardson (1919).

A property of the air being represented by s, the (kinematic) *eddy diffusivity*, K, is defined by the equation

$$\langle \rho V_z' s \rangle = - K \bar{\rho} \, \partial \bar{s} / \partial z. \tag{2}$$

The property s "must be unchanged by the simple transportation of air to a different level" (Richardson), so s may represent such properties as potential temperature and water-vapor concentration (specific humidity or mixing ratio).

The purpose in the formulation of (2) is to express $\langle \rho V_z' s \rangle$ in terms of a factor $\partial \bar{s}/\partial z$ depending only on the mean distribution of s and another factor $K\bar{\rho}$ intended to depend only, or at least primarily, on the turbulent motion. However, no attempt is made to show that $K\bar{\rho}$ depends on the turbulent motion alone, so the eddy diffusivity defined by (2) can also depend on what property s represents. It is reasonable to expect, nevertheless, that the eddy diffusivities of properties having nearly similar vertical distributions are often nearly equal. In the special case that s stands for momentum or velocity (vector or component) the factor K is known as the 'kinematic eddy viscosity' and can be expected, owing to pressure forces on eddies, to differ from the eddy diffusivities to a greater degree.

When the buoyancy term introduced by Ertel is important, *i.e.*, when the property "itself affects the flow, for example, through the action of buoyancy forces" (Priestley and Swinbank, 1937a), the eddy diffusivities defined by (2) may be different for different properties and, indeed, for some property in some region the eddy diffusivity may be negative. The buoyancy term is presumably large for potential temperature when the atmosphere is receiving heat by contact with an underlying warm surface. However, this condition does not appear to necessitate that the eddy diffusivities for potential temperature and water-vapor concentration be different, because, especially if the surface is water of constant temperature, the mean vertical distributions may be similar and the local correlation between temperature and water-vapor concentration may be nearly perfect.

3. Energy flux from an open system

A simple initial problem is to formulate the eddy flux of water vapor. If q represents specific humidity, the upward eddy flux of mass of water vapor through unit area of a horizontal surface moving upward at speed V_z is $\langle \rho V_z' q \rangle$. It follows from (2) that

$$\langle \rho V_z' q \rangle = - K \bar{\rho} \, \partial \bar{q} / \partial z. \tag{3}$$

For heat flux the expressions corresponding to the left side of (3) are not so obvious. Taylor (1915, p. 2) stated that "the rate at which heat is propagated across any horizontal area" is $\int\int \sigma \rho v_z T dx dy$, where σ is "specific heat," but he failed to say which specific heat. Priestley and Swinbank (1947b) start by stating,

without explanation, that the heat flux per unit area is $c_v\bar{\rho}\langle v_z T'\rangle$, where c_v is specific heat at constant volume, and then add a "rate of working"

$$p\bar{v}_z = (c_p - c_v)\bar{\rho}\langle v_z T'\rangle,$$

where p is pressure; the sum is the "total flux of energy" $c_p\bar{\rho}\langle v_z T'\rangle$. Although these results may be considered correct, they have been reached by methods which are not entirely satisfactory. The difficulty may be traced to the fact that 'heat flux' acquires a specific meaning only in terms of the effects occurring in a clearly delimited system.

The first step is therefore to delimit a thermodynamic system which supplies the heat flux at a given point. Let the system, designated O, be a layer of the atmosphere bounded below by the ground, bounded above by a surface which at time t is horizontal and contains the given point but which moves upward at each point with the local value of the speed V_z, and bounded laterally by a material surface. An element of the upper surface has the area dS, and the entire upper surface has the area $\int\int dS = S$. The area S is sufficiently large so that the instantaneous mass flux out of the top is negligible;

$$\int\int \rho V_z' \, dS = 0. \tag{4}$$

Consequently the total mass of the system is constant (except for comparatively small amounts of water gained from the ground or lost by precipitation, and so forth). The pressures in the system and its volume and shape may change. Of particular importance is the fact that the composition of the system can alter by exchange of material through the upper surface. Such a system, having a boundary permeable to matter, is known as an *open system*.

The subject of the thermodynamics of open systems is familiar to heat engineers and has been applied by the Belgian scientists van Lerberghe and Glansdorff (1936) and Van Mieghem (1941; 1943) to the growth of raindrops and to wet-bulb thermometers. However, the subject has not previously been applied to eddy diffusion in the atmosphere and is unfamiliar to most meteorologists. The present treatment, rather than starting from general theorems concerning open systems, starts with the first law of thermodynamics stated for closed systems and leads to its statement in a form pertaining to the open system O as a special case. The treatment is similar in type to that used by Keenan (1941, p. 32).

If a closed system in the time interval Δt receives an amount of heat Q and does an amount of work W, the internal energy of the system increases by an amount ΔE given by

$$Q = \Delta E + W. \tag{5}$$

For an open system this formulation of the first law is, in general, incomplete.

Consider the closed system, designated C, which coincides with system O at time t. At time $t + \Delta t$, system C consists of system O plus the masses that leave through the upper surface of system O during Δt. Some of these masses are positive, some negative, and their sum, according to (4), is

$$\Delta t \int\int \rho V_z' \, dS = 0. \tag{6}$$

For system C, (5) may be written

$$Q_C = \Delta E_C + W_C. \tag{7}$$

The increase in internal energy of system C during the interval Δt equals the increase in internal energy of system O during Δt plus the internal energy at time $t + \Delta t$ of all the masses that leave system O during Δt. The internal energies of these masses change somewhat from the times of leaving system O until $t + \Delta t$. Let specific internal energy be represented by e. The average time when the masses leave is $t + \frac{1}{2}\Delta t$, so the sum of their internal energies at time $t + \Delta t$ may be written

$$\Delta t \int\int \rho V_z' \left(e_{t+\frac{1}{2}\Delta t} + \frac{de}{dt}\tfrac{1}{2}\Delta t \right) dS.$$

The second term in this expression is proportional to $(\Delta t)^2$, whereas the first term and, for small values of Δt, both ΔE_C and ΔE_O are proportional to Δt. If Δt is chosen sufficiently small, the term in $(\Delta t)^2$ becomes negligible and

$$\Delta E_C = \Delta E_O + \Delta t \int\int \rho V_z' e \, dS. \tag{8}$$

The work of expansion of the upper surface of system C is

$$\Delta t \int\int v_z p \, dS = \Delta t \int\int V_z p \, dS + \Delta t \int\int V_z' p \, dS,$$

the right side resulting from (1). The last term is the amount by which the work of expansion of system C exceeds the work of expansion of system O, so

$$W_C = W_O + \Delta t \int\int V_z' p \, dS. \tag{9}$$

If α represents specific volume, (7–9) yield

$$Q_C - \Delta t \int\int \rho V_z'(e + p\alpha) dS = \Delta E_O + W_O. \tag{10}$$

This equation is a statement of the first law for the open system O. During time Δt, system O increases in internal energy by ΔE_O (exhibited by increases in temperature, height, speed, *etc.*) and does the work

W_0 (including expansion and transfer of mechanical energy to oceanic drift currents or to windmills). The sum of these energies equals the heat Q_C (absorption of radiation within the layer and conduction from the ground) received during Δt by a closed system C which initially coincides with system O (this heat can be considered to be the heat Q_0 received by system O) less the energy

$$\Delta t \iint \rho V_z'(e + p\alpha) dS.$$

This energy may properly be called the *eddy transfer of energy* through the upper surface of system O. Consequently, the *eddy flux of energy* may be defined as

$$\iint \rho V_z'(e + p\alpha) dS = S\langle \rho V_z'(e + p\alpha)\rangle.$$

The internal energy may be limited to three forms: kinetic energy, potential energy, and 'thermal' internal energy. Then

$$e = \tfrac{1}{2}v^2 + \phi + u, \tag{11}$$

where v is speed, ϕ is geopotential, and u is the specific internal energy of the same fluid at the same pressure and temperature but in the absence of motion, geopotential, and other effects. Now

$$\langle \rho V_z'\phi\rangle = \phi\langle \rho V_z'\rangle = 0,$$

and the *specific enthalpy*,[2] h, is defined as

$$h = u + p\alpha. \tag{12}$$

Hence the eddy flux of energy per unit area is

$$\tfrac{1}{2}\langle \rho V_z'v^2\rangle + \langle \rho V_z'h\rangle.$$

The first term is the eddy flux of kinetic energy per unit area. The *eddy flux of heat per unit area* may be defined as the term $\langle \rho V_z'h\rangle$. The fluxes are positive when directed upward.

4. Eddy flux of heat and eddy diffusivity

Let Y be specific enthalpy plus geopotential:

$$Y = h + \phi. \tag{13}$$

If a parcel having specific enthalpy h and specific volume α' is displaced vertically and isentropically in a hydrostatic environment of specific volume α, $dh = \alpha' dp$, and the hydrostatic equation gives $d\phi = -\alpha\, dp$. Hence, for the parcel,

$$dY = dh + d\phi = (\alpha' - \alpha)dp.$$

Therefore, except for the negligible change due to the difference in specific volume between parcel and environment, the function Y is unchanged by simple vertical displacement of the parcel.

Substitution of Y for s in (2) yields

$$\langle \rho V_z'h\rangle = -K\bar{\rho}\,\partial\bar{Y}/\partial z, \tag{14}$$

which is a general formulation of the unit-area eddy flux of heat in terms of the eddy diffusivity.

Dry air, water vapor, and their mixture will be treated as perfect gases with constant specific heats.

5. Case I: latent heat neglected

In this section the water-vapor concentration is assumed to be constant. Specific enthalpy is consequently a function of temperature alone. A further consequence is that the mean molecular weight m and the isobaric specific heat c_p are constants for any given situation.

Specific enthalpy is therefore c_pT—plus an arbitrary constant, which in this section is set equal to zero. The unit-area eddy flux of heat becomes $c_p\langle \rho V_z'T\rangle$. The function Y becomes

$$Y_d = c_pT + \phi, \tag{15}$$

the quantity which, when used for another purpose, has been called 'isentropic acceleration potential' (Montgomery and Spilhaus, 1941). From (14),

$$c_p\langle \rho V_z'T\rangle = -K\bar{\rho}\,\partial\bar{Y}_d/\partial z, \tag{16}$$

a general formulation of the unit-area eddy flux of heat for constant water-vapor concentration.

When the water-vapor concentration is variable, (16) represents approximately the part of the flux that is not due to the eddy flux of water vapor and of latent heat. This part may be called the *unit-area eddy flux of sensible heat.*

The right side of (16) can be expressed in terms of the lapse rate of temperature. The mean of (15) is $\bar{Y}_d = c_p\bar{T} + \phi$, so

$$\frac{\partial\bar{Y}_d}{\partial z} = c_p\left(\frac{\partial\bar{T}}{\partial z} + \frac{g}{c_p}\right),$$

where $g = \partial\phi/\partial z$ is gravity. The quantity g/c_p equals the adiabatic lapse rate of temperature. Thus

$$c_p\langle \rho V_z'T\rangle = -c_pK\bar{\rho}\left(\frac{\partial\bar{T}}{\partial z} + \frac{g}{c_p}\right). \tag{17}$$

The expression on the right was first presented by Schmidt (1921, p. 263) and later by Brunt (1929, 1939).

An expression in terms of the lapse rate of potential temperature is obtained more easily by returning to (2). Substitution of $c_p\theta$ for s yields

$$c_p\langle \rho V_z'\theta\rangle = -c_pK\bar{\rho}\,\partial\bar{\theta}/\partial z. \tag{18}$$

[2] The word 'enthalpy' was first used in meteorology by van Lerberghe and Glansdorff (1936) but is still not in common meteorological use and Normand (1946, p. 146) comments: "Personally I have no liking for the word enthalpy and so continue to use the older term of total heat."

Because air is assumed to be a perfect gas,

$$\frac{T}{\theta} = \left(\frac{p}{p_0}\right)^{\kappa}, \qquad \kappa = \frac{R}{mc_p}, \tag{19}$$

where p_0 is the standard pressure. The quantity κ is constant. If the turbulent fluctuation of pressure at a fixed point is neglected in comparison with that of temperature,

$$\frac{\bar{T}}{\bar{\theta}} = \left(\frac{\bar{p}}{p_0}\right)^{\kappa} \tag{20}$$

Hence $T/\theta = \bar{T}/\bar{\theta}$, so that (18) becomes

$$c_p\langle \rho V_z' T\rangle = -c_p K\bar{\rho}\frac{\bar{T}}{\bar{\theta}}\frac{\partial\bar{\theta}}{\partial z}. \tag{21}$$

The expression on the right is given without derivation by Burke (1945, p. 97). The expression given by Taylor (as mentioned in section 1) and repeated by Lettau (1939, p. 142), in which the factor $\bar{T}/\bar{\theta}$ is lacking, is correct only when the standard pressure is not very different from the actual pressure.

6. Case II: latent heat included

Expressions for the eddy flux of heat

If the specific enthalpy including the heat latent in the water vapor is represented by h_t, the unit-area eddy flux of heat including latent heat is $\langle \rho V_z' h_t\rangle$. Let

$$Y_t = h_t + \phi, \tag{22}$$

so (14) becomes

$$\langle \rho V_z' h_t\rangle = -K\bar{\rho}\,\partial\bar{Y}_t/\partial z, \tag{23}$$

a general formulation of the unit-area eddy flux of heat including latent heat

The quantity Y_t defined by (22) embodies Kiefer's (1941) suggestion that the function Y_d be extended "to include the vapor energy and so enhance appreciably the effectiveness of that function in meteorological analyses."

It follows from the Gibbs-Dalton law that the enthalpy of a mixture of two gases equals the sum of the enthalpies of the components each alone having the temperature and volume of the mixture. Hence the specific enthalpy of air having specific humidity q equals the sum of $(1 - q)$ times the specific enthalpy of dry air and of q times the specific enthalpy of water vapor. The specific enthalpy of dry air having isobaric specific heat c_{pd} is a constant plus $c_{pd}T$. The specific enthalpy of water vapor having isobaric specific heat c_{pw} is a constant plus $c_{pw}T$.[3]

[3] This linear relation is a good approximation for the meteorological range of conditions. The specific enthalpy of saturated water vapor tabulated by Kiefer from −73C to +50C increases by 222 j g^{-1} but deviates by no more than 1 j g^{-1} from a linear function of temperature. In the same range, −100F to +120F, the more detailed values in engineering units in table 2 of chapter 3 of the *Heating, ventilating, air conditioning guide 1947* of the American Society of Heating and Ventilating Engineers deviate by only 0.6 j g^{-1}.

The arbitrary constants are conveniently specified, in the present problem, by assigning zero enthalpy to both dry air and saturated water or ice at an arbitrary absolute temperature T_0. The specific enthalpy of dry air at absolute temperature T becomes $c_{pd}(T - T_0)$. The specific enthalpy of saturated vapor at T_0 equals L_0, the latent heat of vaporization or sublimation, as the case may be, at T_0; hence the specific enthalpy of water vapor at absolute temperature T is

$$L_0 + c_{pw}(T - T_0).$$

Finally, since

$$c_p = (1 - q)c_{pd} + qc_{pw}, \tag{24}$$

$$h_t = c_p(T - T_0) + L_0 q \tag{25}$$

and

$$Y_t = c_p(T - T_0) + L_0 q + \phi. \tag{26}$$

If equivalent temperature is defined in a special manner, it offers another means as exact as (23) of expressing the eddy flux of heat. For this purpose, the *equivalent temperature* of a sample of air is defined as the temperature of dry air having the same specific enthalpy. Hence, from (25), if the absolute equivalent temperature is represented by T_e,

$$h_t = c_p(T - T_0) + L_0 q = c_{pd}(T_e - T_0). \tag{27}$$

It may be noted that specific enthalpy and equivalent temperature are here expressed as linear functions of one another; furthermore

$$\langle \rho V_z' h_t\rangle = c_{pd}\langle \rho V_z' T_e\rangle. \tag{28}$$

From (22) and (27),

$$Y_t = c_{pd}T_e + \phi, \tag{29}$$

the constant term $c_{pd}T_0$ being omitted because only the gradient of Y_t, not Y_t itself, occurs in the expression (23) for heat flux. It may be noted that Y_t in (29) is similar in form to Y_d in (15). The mean of (29) is $\bar{Y}_t = c_{pd}\bar{T}_e + \phi$, so

$$\frac{\partial\bar{Y}_t}{\partial z} = c_{pd}\left(\frac{\partial\bar{T}_e}{\partial z} + \frac{g}{c_{pd}}\right).$$

The quantity g/c_{pd} is not quite the adiabatic lapse rate, g/c_p, but is, conveniently, the adiabatic lapse rate that would occur in dry air. Equation (23) becomes

$$\langle \rho V_z' h_t\rangle = -c_{pd}K\bar{\rho}\left(\frac{\partial\bar{T}_e}{\partial z} + \frac{g}{c_{pd}}\right). \tag{30}$$

The right side of (23) or (30) can be expressed approximately in terms of the lapse rate of *equivalent potential temperature*, which is defined as the equivalent temperature the air would attain if changed

isentropically to standard pressure. Let θ_e represent absolute equivalent potential temperature. Substitution of θ_e for s in (2) gives

$$c_{pd}\langle \rho V_z' \theta_e \rangle = - c_{pd} K \bar{\rho} \partial \bar{\theta}_e / \partial z. \quad (31)$$

From (27) and the definition of equivalent potential temperature,

$$c_p(\theta - T_0) + L_0 q = c_{pd}(\theta_e - T_0). \quad (32)$$

From (27) and (32),

$$c_{pd}(T_e - \theta_e) = c_p(T - \theta). \quad (33)$$

On being multiplied by $\rho V_z'$ and averaged, this equation becomes

$$c_{pd}\langle \rho V_z' T_e \rangle - c_{pd}\langle \rho V_z' \theta_e \rangle = \langle c_p \rho V_z' \theta [(T/\theta) - 1] \rangle.$$

In view of (19), if the fluctuation of $(p/p_0)^\kappa$ is neglected,

$$c_{pd}\langle \rho V_z' T_e \rangle = c_{pd}\langle \rho V_z' \theta_e \rangle + [(\bar{p}/p_0)^\kappa - 1]\langle c_p \rho V_z' \theta \rangle.$$

When the standard pressure is not very different from the actual pressure, the last term is relatively small and may be neglected; then substitution of (28) and (31) gives

$$\langle \rho V_z' h_t \rangle = - c_{pd} K \bar{\rho} \partial \bar{\theta}_e / \partial z. \quad (34)$$

The expression on the right was first presented by Schmidt (1921, p. 266) and has been used by Raethjen (1941).

Specification of the temperature T_0

It is significant that the heat flux $\langle \rho V_z' h_t \rangle$ depends on the arbitrary quantity T_0. This sort of dependence is inherent in a problem dealing with unsteady flow in a medium of variable composition, because there is an arbitrary constant in the enthalpy scale of each component. The quantity T_0 is the absolute temperature at which equal masses of dry air and saturated water or ice have the same (zero) enthalpy. In general, the eddy flux of heat at a point cannot be specified absolutely in terms of the local phenomena (V_z', T, q, *etc.*) alone.

To find the degree of dependence on T_0, the heat flux may be written, from (24) and (25),

$$\langle \rho V_z' h_t \rangle = \langle c_p \rho V_z' T \rangle + [L_0 - (c_{pw} - c_{pd})T_0]\langle \rho V_z' q \rangle. \quad (35)$$

The factor in brackets is a function of T_0. If the isobaric specific heat of liquid water or ice is c_w,

$$dL_0/dT_0 = - (c_w - c_{pw}) \quad (36)$$

(see, for instance, Holmboe, Forsythe, Gustin, 1945, p. 47), so

$$\frac{d \ln[L_0 - (c_{pw} - c_{pd})T_0]}{dT_0} = - \frac{c_w - c_{pd}}{L_0 - (c_{pw} - c_{pd})T_0}. \quad (37)$$

Insertion of numerical values on the right side of this equation gives the result that, for liquid water at $T_0 = 273$C, the factor $[L_0 - (c_{pw} - c_{pd})T_0]$ decreases by 0.14 per cent for an increase of 1C in T_0. It therefore appears that for practical purposes a change of a few degrees in T_0 is insignificant, but that an accurate calculation of heat flux depends on knowing the proper value of T_0 within a few tens of degrees.

A proper value to assign to T_0 is the temperature of surfaces of water or ice in the layer described in section 3. This conclusion becomes apparent if system O is further defined to include underlying surfaces of ground, water, or ice and to include surfaces of all drops or snowflakes but to exclude all ground, water, or ice except a surface film. Then condensation or evaporation at these surfaces occurs within system O, which simply experiences a loss or gain of water or ice of zero enthalpy. Hence (10) remains a complete statement of the conservation of energy.

The fact that all condensation and evaporation within the layer may not be at one temperature offers no practical difficulty in the choice of T_0. The heat flux is not sensitive to small changes of T_0, so an average or approximate value of T_0 is adequate. However, if surfaces of both water and ice exist in the layer, special provisions might be needed to achieve adequate accuracy.

Wet-bulb temperature

Let T_w represent absolute wet-bulb temperature, w represent actual mixing ratio, w_w represent saturation mixing ratio at the wet-bulb temperature and actual pressure, and L_w represent latent heat of vaporization at the wet-bulb temperature. Then wet-bulb temperature is determined by the psychrometric formula

$$(c_{pd} + w c_{pw})(T - T_w) = L_w(w_w - w) \quad (38)$$

(see, for instance, Montgomery, 1948, eq. 1).

According to one definition, the *equivalent temperature* of a sample of air is the temperature of dry air at the same pressure and wet-bulb temperature. If the absolute equivalent temperature so defined is represented by T_{ew}, (38) gives

$$c_{pd} T_{ew} = c_{pd} T_w + L_w w_w. \quad (39)$$

This absolute 'wet-bulb' equivalent temperature T_{ew} may be compared with the absolute 'specific-enthalpy' equivalent temperature T_e occurring in (27–34) if T_0 is set equal to T_w. The temperature T_{ew} is slightly higher than T_e, because the basis of T_{ew} is that the enthalpy of unit mass of dry air at absolute temperature T_{ew} is equal to the enthalpy of $(1 + w)$ times unit mass, instead of the enthalpy of unit mass, of moist air at absolute temperature T; the difference between the two equivalent temperatures, for a given

pressure and wet-bulb temperature, is proportional to the mixing ratio. Both wet-bulb temperature and 'wet-bulb' equivalent temperature are conservative for isobaric, adiabatic evaporation of water at the wet-bulb temperature (proposition IV by Normand, 1921). During such evaporation w increases but the enthalpy of $(1 + w)$ times unit mass of moist air remains constant, so the specific enthalpy decreases slightly and T_e also decreases slightly. The quantity T_e, which is uniquely suited for heat-flux equations, therefore has the disadvantage of being not quite conservative during evaporation. Furthermore, being a function of T, q, and T_0, it is less easily computed from psychrometric observations than is T_{ew}, which is a function of pressure and wet-bulb temperature only.

Wet-bulb potential temperature is defined as the wet-bulb temperature which the air would attain if changed isentropically to standard pressure. The absolute wet-bulb potential temperature θ_w is related to the absolute potential temperature θ, according to (38), by

$$(c_{pd} + wc_{pw})(\theta - \theta_w) = L_{wp}(w_{wp} - w), \quad (40)$$

where L_{wp} is the latent heat of vaporization at absolute temperature θ_w and w_{wp} is the saturation mixing ratio at absolute temperature θ_w and standard pressure.

If the absolute 'wet-bulb' equivalent potential temperature is represented by θ_{ew}, (40) gives

$$c_{pd}\theta_{ew} = c_{pd}\theta_w + L_{wp}w_{wp}. \quad (41).$$

The right side of this equation is a function of θ_w alone Since θ_w and θ_{ew} are increasing functions of one another and since $\theta_{ew} \approx \theta_e$, the approximate qualitative result is obtained from (34) that, according as $\partial\bar{\theta}_w/\partial z \gtreqless 0$, the eddy flux of heat is upward, zero, or downward—if the standard pressure is close to the actual pressure and if the eddy diffusivity is positive. Quantitatively, however, to neglect the last term in (41), thus obtaining

$$\langle \rho V_z' h_t \rangle = - c_{pd} K \bar{\rho}\, \partial\bar{\theta}_w/\partial z,$$

would be in great error: at a wet-bulb potential temperature of 0C, $d\theta_e/d\theta_w = 1.7$; at 30C, $d\theta_e/d\theta_w = 4.7$ (standard pressure 1000 mb).

7. Eddy flux of heat from dry ground

This section and the following one are based on the assumption that there is a certain boundary layer within which the vertical variation of eddy flux is negligible. This layer may be called the *constant-flux boundary layer*. Such an assumption permits equations (16, 17, 21, 23, 30, 34) to be integrated to give the heat flux as the product of (a) a factor depending on the vertical distribution of eddy diffusivity and (b) the difference in a measurable quantity at two levels within the constant-flux layer (43–48).

While a constant-flux boundary layer probably does not always exist, there appear to be common circumstances when it does. Equation (10), expressing the conservation of energy for system O, may be written, if $e + p\alpha$ is specialized to h and if the work W_O is neglected,

$$S\langle \rho V_z' h \rangle = Q_C/\Delta t - \Delta E_O/\Delta t. \quad (42)$$

Therefore, if the right side of this equation is constant with the thickness of system O up to a certain limit, the flux $S\langle \rho V_z' h \rangle$ is constant with height up to the same limit. For a sufficiently thin system, the rate of change of energy $\Delta E_O/\Delta t$ may be neglected compared with the eddy flux of heat; the system is thus regarded as being in a steady state. The quantity $Q_C/\Delta t$ is the rate at which heat is gained by radiation absorption within the system and by conduction upward across the base (which was specified in section 6 to lie immediately below the ground or water surface). In the circumstances studied by Panofsky (1947), the rate at which radiation is absorbed by the gaseous part of the system is no larger than $\Delta E_O/\Delta t$, which has already been neglected; the remaining absorption of radiation occurs at the ground or water surface and does not vary with the thickness of system O.

Suppose, in the present section, that the underlying surface is dry ground. The water-vapor concentration is therefore essentially constant, the general expression for the eddy flux of heat being (16).

Within the constant-flux layer,

$$c_p\langle \rho V_z' T \rangle = - K\bar{\rho}\, \partial\bar{Y}_d/\partial z$$

is constant with height. Integration from $z = a$ to $z = b$, $a < b$, two levels within the constant-flux layer, gives

$$c_p\langle \rho V_z' T \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} (\bar{Y}_{da} - \bar{Y}_{db}). \quad (43)$$

For a given distribution of eddy diffusivity and given heights a and b, the eddy flux of heat from the ground is proportional to $\bar{Y}_{da} - \bar{Y}_{db}$.

Ordinarily the pressures at levels a and b are so close to standard pressure that $\bar{T}/\bar{\theta} = 1$ is an adequate approximation in (21); a difference of 10 per cent between p and p_0 causes the factor $\bar{T}/\bar{\theta}$ to deviate from unity by only 3 per cent. It follows, in the same way that (43) follows from (16), that

$$c_p\langle \rho V_z' T \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} c_p(\bar{\theta}_a - \bar{\theta}_b). \quad (44)$$

If the levels a and b are both close to the ground, the adiabatic lapse rate may be neglected in comparison with the actual lapse rate, so that (17) gives

$$c_p\langle \rho V_z' T \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} c_p(\bar{T}_a - \bar{T}_b). \quad (45)$$

If the difference between a and b is 10 m, $(\bar{T}_a - \bar{T}_b)$ is only 0.1C greater than $\bar{\theta}_a - \bar{\theta}_b$.

The ground is coated by a *laminar sublayer*, of the order of one millimeter in thickness. If the level a is chosen to be at the ground, (43–45) must be modified by replacing the eddy diffusivity K within the laminar layer with the thermometric conductivity. The form of (43–45), however, is not changed. The eddy flux of heat from the ground is proportional to $\bar{Y}_{da} - \bar{Y}_{db}$ or approximately to $\dot{\theta}_a - \bar{\theta}_b$ or to $\bar{T}_a - \bar{T}_b$, where the first quantity in each difference is the appropriate property of the air in immediate contact with the ground.

8. Eddy flux of heat from water or moist ground

If the underlying boundary is wet instead of dry, the general expression (23) for the eddy flux of heat contains Y_t in place of Y_d, so the unit-area eddy flux of heat from the surface is

$$\langle \rho V_z' h_t \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} (\bar{Y}_{ta} - \bar{Y}_{tb}), \qquad (46)$$

valid for any two levels a and b within the constant-flux boundary layer but outside the laminar sublayer.

Since (46) depends on the flux of both water vapor and sensible heat, the eddy diffusivity K cannot, strictly, be replaced by a single property in the laminar layer, where the thermometric conductivity and the diffusivity of water vapor in air are distinct physical quantities. The approximation is nevertheless made that (46) is valid even when level a coincides with the underlying wet surface. A definite error is thus introduced, but it is of the nature of a small, omitted correction. In two theoretical examples (Montgomery, 1940, figs. 6, 8) the change of humidity across the laminar layer is about 20 per cent of the total change from a water surface (a) up to a level (b) of 1–10 m; since diffusivity is 19 per cent greater than conductivity (Montgomery, 1947), the order of magnitude of the error in the flux of sensible heat or latent heat is therefore 4 per cent. When $\langle \rho V_z' h_t \rangle = 0$, $\partial \bar{Y}_t / \partial z$ is zero above the laminar layer but is greater than zero within the laminar layer. When $\langle \rho V_z' h_t \rangle = 0$ and level a coincides with the wet surface, $\bar{Y}_{ta} - \bar{Y}_{tb}$ is therefore negative (zero in the limit $\bar{\theta}_a = \bar{\theta}_b$); if $\bar{\theta}_b - \bar{\theta}_a = 25$C, the value of $(\bar{Y}_{ta} - \bar{Y}_{tb})/c_{pd}$ is about 1C. This comparatively small value is an illustration of the error introduced by assuming that (46) is valid even when level a coincides with the wet surface. In very light winds the error is greater.

Less general expressions than (46) are good approximations under certain conditions. If the pressures are, say, within 10 per cent of the standard pressure and if certain approximations are allowed,

$$\langle \rho V_z' h_t \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} c_{pd} \langle \bar{\theta}_{ea} - \bar{\theta}_{eb} \rangle, \qquad (47)$$

which follows directly from (34). If the levels a and b are closer to the ground than, say, 10 m, the last term in (30) is negligible and the result is obtained that

$$\langle \rho V_z' h_t \rangle = \left(\int_a^b \frac{dz}{K\bar{\rho}} \right)^{-1} c_{pd} (\bar{T}_{ea} - \bar{T}_{eb}). \qquad (48)$$

The quantity T_0, on which Y_t, θ_e, and T_e in these expressions depend, is the absolute temperature at the wet surface, because the evaporation or condensation occurs there (see the second part of section 6). A rough value for T_0 is adequate.

Since wet-bulb temperature is not a linear function of equivalent temperature, the heat flux is not proportional to a difference of two wet-bulb temperatures. Wet-bulb temperature is directly measurable and may, however, be used qualitatively to reveal the sense of the heat flux. It follows from the corresponding conclusion in the last part of section 6, if the eddy

TABLE 1. Equivalent temperature, centigrade, of air at centigrade temperature t and 1000 mb at a surface of ice (t_{ei}), water (t_e), and sea water (t_s). Equivalent temperature t_{ei} is based on latent heat of sublimation L_i, t_e is based on latent heat of vaporization L. The table includes vapor pressure e and specific humidity q and, in the third case, centigrade wet-bulb temperature t_w.*

	Ice				Water				Sea water, salinity 35 per mille				
t C	e mb	q per mille	L_i j g^{-1}	t_{ei} C	e mb	q per mille	L j g^{-1}	t_e C	e mb	q per mille	t_e C	t_w C	t C
40	—	—	—	—	73.7	47.13	2407	153.0	72.3	46.21	150.8	39.70	40
30	—	—	—	—	42.43	26.81	2431	94.93	41.63	26.29	93.66	29.74	30
20	—	—	—	—	23.37	14.66	2454	55.82	22.93	14.38	55.14	19.79	20
10	—	—	—	—	12.28	7.67	2478	28.93	12.05	7.53	28.57	9.84	10
0	6.105	3.80	2835	10.74	6.105	3.80	2502	9.48	5.99	3.73	9.30	− 0.11	0
−10	2.60	1.62	2837	− 5.43	2.86	1.78	2526†	− 5.52	2.81	1.75	−5.60	−10.06	−10
−20	1.04	.65	2839	−18.17	1.24	.77	2550†	−18.04	—	—	—	—	−20
−30	.381	.24	2840	−29.33	—	—	—	—	—	—	—	—	−30
−40	.131	.08	2939	−39.77	—	—	—	—	—	—	—	—	−40

* Saturation vapor pressure and latent heats are from Kiefer's (1941) table. The vapor pressure over salt water is based on a relative humidity of 98.12 per cent (Sverdrup, Johnson, Fleming, 1942, p. 115). Specific humidity has been computed from vapor pressure. Equivalent temperature has been computed from $T_{ei} = T + (L_i/c_{pd})q$ and $T_e = T + (L/c_{pd})q$, which are obtained from eq. (27) on setting $T_0 = T$; $c_{pd} = 1004$ j g^{-1}.

† From Kiefer's (1941) eq. (5).

diffusivity is positive and if the pressures are within, say, 10 per cent of standard pressure, that $\langle \rho V_z' h_t \rangle \gtreqless 0$ according as $\bar{\theta}_{wa} \gtreqless \bar{\theta}_{wb}$. If the levels a and b are closer to the surface than, say, 10 m, $\langle \rho V_z' h_t \rangle \gtreqless 0$ according as $\bar{T}_{wa} \gtreqless \bar{T}_{wb}$.

It may be noted that the derivations of (43–48) and of the qualitative results do not entail any assumption that the surface temperature does not fluctuate in time and space.

At an underlying boundary of pure water the vapor is saturated, the wet-bulb temperature equals the temperature, and the equivalent temperature is a function of temperature and pressure only. At a boundary of salt water the vapor is unsaturated, the wet-bulb temperature is lower than the temperature, and the equivalent temperature is lower than it is at a surface of pure water at the same temperature and pressure; the value of each depends on the salinity. A few representative values are given in table 1. The equivalent temperatures given for an ice surface have been computed from the latent heat of sublimation; when the surface is ice, the values of Y_t, θ_e, and T_e at both levels (a, b) must, of course, be based on the latent heat of sublimation, *i.e.*, the enthalpy of ice and of dry air are both arbitrarily zero at the temperature of the surface. Over the ocean, the latent heat of vaporization from salt water is appropriate; however, it is only 0.1 per cent greater than for pure water, so the latent heat of vaporization from pure water has been used in computing the equivalent temperatures at a salt-water surface.

Equations (46–48) offer a direct method of estimating the total eddy flux of heat from an ice or water surface. These equations obviate the need to estimate separately the fluxes of sensible heat and latent heat and may be used in place of such separate equations as those given by Sverdrup, Johnson, and Fleming (1942, pp. 114–117) and used by Jacobs (1942) in computing the heat flux from ocean to atmosphere. It can reasonably be expected that the first factor on the right of equations (46–48) is the same as the factor occurring in equations for the separate eddy fluxes of sensible heat and water vapor (*cf.* section 2). The method presented here is advantageous because the basic data, which are usually temperatures and wet-bulb temperatures, can be reduced directly to equivalent temperatures without computing any other humidity.

It has been customary to regard heat transfer by conduction across the ocean surface and heat transfer by evaporation or condensation as two physical entities, the warming or cooling of the ocean being obtained by combining the effects of these processes and of radiation, three in all. The present results show that the first two calculations can be replaced by one. Furthermore, both of these supposedly separate processes are, from the point of view of kinetic theory, manifestations of molecular interaction at the air-water boundary and can be regarded as a single entity. In the special case of zero temperature gradient in the air next to the boundary, the eddy transfer of heat equals the latent heat of the evaporated water. In the special case of no net transfer of water molecules, the heat transfer is properly called 'heat conduction.' In the general case, however, there is a transfer of water and a transfer of heat; to separate this heat, manifested by the warming or cooling of the ocean, into conduction and latent heat of evaporation appears artificial. The ocean is warmed or cooled by two processes: radiation and what may perhaps be called 'contact.'

Acknowledgments.—Assistant Professor P. A. Sheppard of the Imperial College of Science and Technology, during a visit to Woods Hole in September 1947, kindly read a draft of the paper and made suggestions leading to improvements. After the paper was submitted for publication the writer was permitted to incorporate further changes resulting from helpful criticism by Professor Paul J. Kiefer of the U. S. N. Postgraduate School.

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Contribution No. 407

EVALUATION OF SEA-SURFACE ROUGHNESS FROM UNDERWATER-PRESSURE RECORDINGS

H. R. Seiwell

(Contribution No. 407, Woods Hole Oceanographic Institution)

A total of 639 records of underwater-pressure fluctuations from Woods Hole vicinity off Cuttyhunk Island, Massachusetts, and 1022 records from Bermuda, has been evaluated in terms of sea-surface roughness. The Woods Hole (Cuttyhunk) records cover the period July 1946 to May 1947, with operational times of 20 minutes every four hours; and the Bermuda records, February to May 1947, with operational times 20 minutes every two hours.

Average and modal values of wave heights and wave periods together with standard deviations and probable errors are tabulated for each month. Relationships between the average wave height and period, average of the highest one-third waves, highest waves and wave steepness are also shown.

The study is preliminary and present results are intended to illustrate the type of sea-surface data to be obtained from recently developed wave-recording instruments.

Introduction

Underwater-pressure instruments, which automatically record pressure changes near the sea bottom, are in operation in the vicinity of Woods Hole (off Cuttyhunk Island, Massachusetts) and Bermuda. At both locations the pressure elements are located on the sea bottom (approximate depth 75 feet at Cuttyhunk and 120 feet at Bermuda) and electrically connected to onshore recorders by cable. The present operational schedule is a continuous 20-minute recording every two hours at Bermuda and every four hours at Cuttyhunk.

Records from these instruments are scaled for pressure wave height (ΔH_h) and wave period (T) at depth of instrumentation, h. The wave height at the sea surface (ΔH_s) is then computed by

$$\Delta H_s = 1.35 \Delta H_h \cosh 2\pi h/\lambda \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where

$$\lambda = gT^2/2\pi \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

In (1), the factor 1.35 has been experimentally determined at both instrument sites, by direct comparison of simultaneous near-bottom and surface-wave heights [see "References" at end of paper, SEIWELL, 1947 and SEIWELL (in press)]. Its probable error is 0.037.

A total of 639 records from Cuttyhunk and 1022 from Bermuda has been analyzed. In each case, two-minute intervals of each record were scaled for wave height and wave period and the average of each computed. On the basis of arrangements into monthly frequency distributions, the characteristic statistics computed are summarized in Tables 1 and 2.

The sea surface at Cuttyhunk and Bermuda

Wave height--Wave height and wave period appear as an inverse relationship, (see Fig. 1), such as would result from longer period waves being generated at such distances from the target that amplitudes are reduced during travel times to values lower than those of the shorter period waves of local winds.

The mean and mode of wave height do not coincide. The most frequently occurring wave heights (indicated by modal values) during any month, are lower than the average monthly wave heights. The difference between mean and mode becomes more for greater wave heights. Thus,

Table 1--Summary of statistical properties of monthly sea-surface conditions at Cuttyhunk

Month	No. of obs.	Sea surface wave height				Bottom wave period			
		Average	Mode	Standard deviation	Probable error	Average	Mode	Standard deviation	Probable error
1946		ft	ft	ft	ft	sec	sec	sec	sec
July	78	1.42	0.67	1.18	0.09	7.99	7.73	1.10	0.08
August	64	1.86	0.99	1.23	0.10	7.73	7.70	1.09	0.09
September	72	0.92	0.56	0.83	0.07	9.51	9.60	1.94	0.16
October	104	1.55	0.70	1.49	0.10	8.62	6.74	1.83	0.12
November	97	1.68	0.93	1.38	0.09	8.22	6.81	1.42	0.10
December	81	3.75	1.09	2.65	0.20	7.46	6.73	1.28	0.10
1947									
March	30	1.12	0.70	0.81	0.03	9.65	8.83	1.80	0.22
April	80	1.42	0.63	1.34	0.10	8.29	8.20	1.37	0.10
May	33	1.27	0.41	0.95	0.11	7.84	6.72	1.95	0.23

Table 2--Summary of statistical properties of monthly sea-surface conditions at Bermuda

Month	No. of obs.	Sea surface wave height				Bottom wave period			
		Average	Mode	Standard deviation	Probable error	Average	Mode	Standard deviation	Probable error
1947									
February	133	1.86	0.80	1.60	0.09	9.63	9.73	0.92	0.05
March	335	1.43	0.77	1.08	0.04	9.58	9.24	1.28	0.05
April	305	0.80	0.70	0.45	0.02	9.83	9.30	1.35	0.05
May	249	0.82	0.71	0.40	0.02	10.33	9.31	1.43	0.06

at Cuttyhunk, where average wave height increased from a value of 0.92 feet in September to 3.75 feet in December, the mode increased from 0.56 to 1.09 feet, a two-fold change in mode compared to a four-fold change of average wave heights. Similarly, at Bermuda, a maximum average wave height of 1.86 in February and a minimum of 0.80 in April had corresponding modal values of 0.80 and 0.70 feet. Thus, winter increases in general roughness of the sea surface are significantly less than increases in average wave height, and the mode is of greater operational value than the average. In forecasting sea-surface roughness, mode and average need be distinguished.

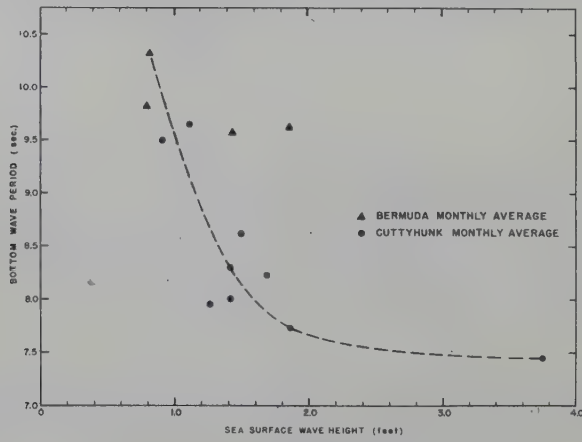

Fig. 1--Relationship of average monthly surface wave height and average bottom wave period for Cuttyhunk and Bermuda

Average wave heights at Bermuda and Cuttyhunk do not differ greatly. During the comparable months of March, April, and May 1947, the average for the former was 1.03 feet compared to 1.27 feet for the latter; modal values were 0.72 and 0.58 feet, respectively. It is indicated that higher seas persist later in the spring along the New England coast.

Wave period--The modal and mean values of bottom wave periods are more nearly equal than in the case of wave heights. Tables 1 and 2 show that the maximum average bottom period of 9.65 in March corresponded with a mode of 8.83 and the minimum average of 7.46 seconds in December had a mode of 6.73. Periods of surface waves are to be expected to be lower than those recorded at or near the bottom. On the basis of simultaneous surface and near-bottom observations in 1946, it was estimated that at depth of instrumentation, the average period at Cuttyhunk was about one-half that occuring at the surface, and at Bermuda about one-third. The average bottom period represents an upper limit for the average surface period.

Relationship of average surface wave height to average of highest one-third waves

The basic measurements of wave heights and wave periods on the records were used to compute averages of the highest one-third waves. These values of greater wave heights are of more operational value than averages of all wave heights in that higher waves dominate conditions during any time interval. Also, it appears that, in visual recordings of waves, it is the highest one-third which is observed, rather than the infinite detail making up the average pattern of the sea surface.

Relationship between average sea surface wave heights and average of the highest one-third waves for Cuttyhunk and Bermuda is illustrated by Figures 2 and 3. The linear relationship is considered significant. For both sets of data, independent fits by least squares give identical results, namely: Average highest one-third waves = 1.57 (average wave height).

Relationship of average wave height to wave steepness

Wave steepness is defined as the ratio of wave height to wave length. It appears to be related to the stage of development of the wave when the latter is expressed as the ratio of wave velocity to wind velocity [U. S. HYDROGRAPHIC OFFICE, 1944].

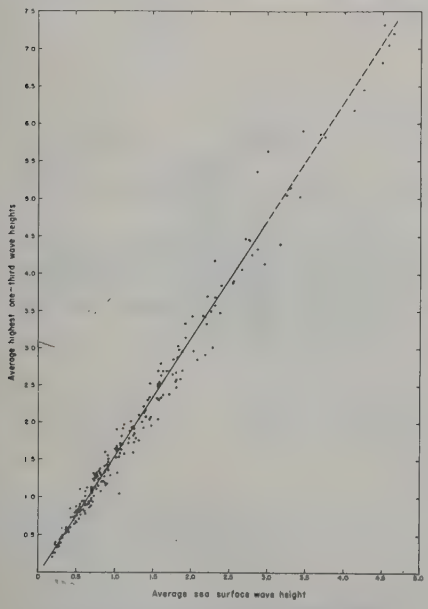

Fig. 2--Relationship average sea-surface wave heights and average highest one-third surface waves, Cuttyhunk

As waves move into shallow water, wave steepness takes on an added significance in that the crests become narrower and steeper after they begin to feel bottom. Thus a shallow-water steepness and a deep-water steepness are distinguished, and the ratio of the two is a characteristic factor in sea-surface conditions.

The critical depth at which wave velocity c is theoretically determined by depth of water h, rather than by length of the wave itself λ, is derived from the basic equation

$$c^2 = gL/2\pi \tanh 2\pi h/\lambda$$

When the ratio of depth to wave length becomes 0.4, deep-water waves begin transformation into shallow-water types. Thus for depth of instrumentation at Cuttyhunk (75 feet), wave lengths above 188 feet (approximately six sec) are affected; and at Bermuda (120 feet) those above 300 feet in length (approximately 7 1/2 sec) are altered. From data in Tables 1 and 2, longer waves occurring at both locations may possibly be expected to have undergone some transformation of their deep-water characteristics.

Wave steepness, as computed for our purposes, is taken as the ratio of average surface wave height to average bottom period. Since the average bottom period represents an upper limit of average surface wave period, the actual average steepness of sur-

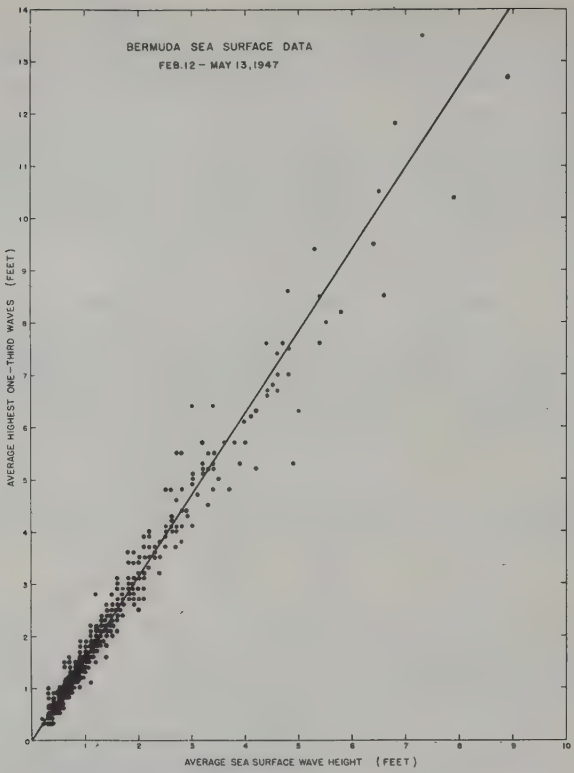

Fig. 3--Relationship average sea-surface wave heights and average highest one-third surface waves, Bermuda

face waves is several times higher. Nevertheless steepness computed in this manner from available records possesses a significance in characterizing the sea surface.

The average values of sea surface wave heights in intervals of 0.5 feet (see Table 3) are plotted against per cent of wave steepness in Figure 4. The least-square straight line fitted to the 900-odd Bermuda values has the equation: Average wave steepness = 0.286 (average wave height) - 0.06. Comparison of computed and observed values for average surface wave heights of 0.04 to 5.41 feet is given in Table 3.

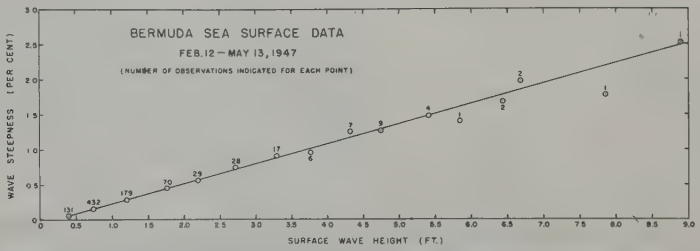
BERMUDA SEA SURFACE DATA
FEB. 12 - MAY 13, 1947
(NUMBER OF OBSERVATIONS INDICATED FOR EACH POINT)
WAVE STEEPNESS (PER CENT)
SURFACE WAVE HEIGHT (FT.)

Fig. 4--Relationship average sea-surface wave heights and average wave steepness, Bermuda; the straight line has the equation: Average wave steepness = 0.29 (average wave height) - 0.06

Table 3--Comparison of observed and computed average wave steepness at Bermuda

Height interval	Average surface wave height	Observed average steepness	Computed average steepness	Difference
ft	ft	pct	pct	pct
0.00-0.50	0.40	0.06	0.06	0.0
0.51-1.00	0.74	0.15	0.16	+ 0.01
1.01-1.50	1.20	0.28	0.29	+ 0.01
1.51-2.00	1.76	0.45	0.45	0.00
2.01-2.50	2.19	0.56	0.57	+ 0.01
2.51-3.00	2.72	0.74	0.72	- 0.02
3.01-3.50	3.29	0.91	0.89	- 0.02
3.51-4.00	3.77	0.96	1.02	+ 0.06
4.01-4.50	4.32	1.25	1.18	- 0.07
4.51-5.00	4.74	1.27	1.30	+ 0.03
5.01-5.50	5.41	1.48	1.49	+ 0.01

Operational surface wave height patterns

On the basis of data analyzed in this fashion, selected statistical parameters may be arranged in patterns of operational value. One type is illustrated by Figure 5, where monthly variations in height limits of significant waves are shown for 50 and 75 per cent time limits.

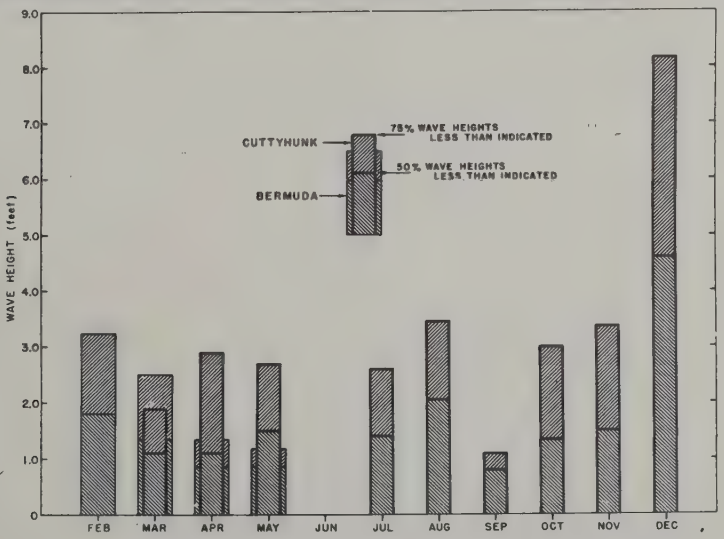

Fig. 5--75 and 50 per cent occurrence of average highest one-third surface waves, Bermuda (February to May 1947) and Cuttyhunk (July to December 1946, March to May 1947)

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(Manuscript received September 30, 1947; presented at the Regional Meeting, Woods Hole, Massachusetts, September 18, 1947; open for formal discussion until September 1, 1948.)

Contribution No. 408

THE WESTWARD INTENSIFICATION OF WIND-DRIVEN OCEAN CURRENTS

Henry Stommel

(Contribution No. 408, Woods Hole Oceanographic Instiution)

Abstract--A study is made of the wind-driven circulation in a homogeneous rectangular ocean under the influence of surface wind stress, linearised bottom friction, horizontal pressure gradients caused by a variable surface height, and Coriolis force.

An intense crowding of streamlines toward the western border of the ocean is discovered to be caused by variation of the Coriolis parameter with latitude. It is suggested that this process is the main reason for the formation of the intense currents (Gulf stream and others) observed in the actual oceans.

Introduction--Perhaps the most striking feature of the general oceanic wind-driven circulation is the intense crowding of streamlines near the western borders of the oceans. The Gulf Stream, the Kuroshio, and the Agulhas Current are examples of this phenomenon. The physical reason for the westward crowding of streamlines has always been obscure. The purpose of this paper is to study the dynamics of wind-driven oceanic circulation using analytically simple systems in an attempt to discover a physical parameter capable of producing the crowding of streamlines.

The phenomenon occurs along coastlines of such varied topography that it is clear that local topographic features do not significantly control the general streamline pattern. For the sake of simplicity the present study deals with flat rectangular oceans.

The formulation of the problem--A rectangular ocean is envisaged with the origin of a cartesian coordinate system at the southwest corner (see Fig. 1). The y axis points northward; the x axis eastward The shores of the ocean are at $x = 0, \lambda$ and $y = 0, b$. The ocean is considered as a homogeneous layer of constant depth D when at rest. When currents occur, as in the real oceans, the depth differs from D everywhere by a small variable amount h. The quantity h is much smaller than D. The total depth of the water column is therefore D + h, D being everywhere constant, and h a variable yet to be determined.

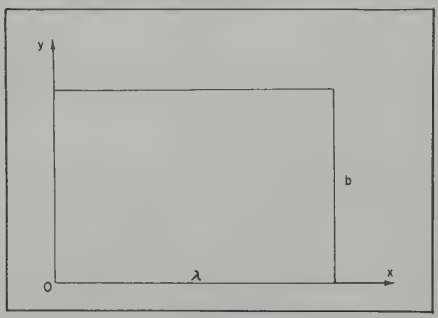

Fig. 1--Ocean basin dimensions and the coordinate system

The winds over the ocean are the Trades over the equatorial half of the rectangular basin, and Prevailing Westerlies over the poleward half. An expression for the wind stress acting upon a column of unit cross-section and depth D + h must include this dependence upon y. A simple functional form of the wind stress is taken as $-F \cos(\pi y/b)$.

In order to keep the ocean from accelerating, a frictional dissipative term is required. To keep the equations of motion as simple as possible the component frictional forces are taken as $-Ru$ and $-Rv$, where R is the coefficient of friction, and u and v are the x and y components of the velocity vector, respectively. The Coriolis parameter f is also introduced. In general it is a function of y.

The steady state equations of motion, with the inertial terms omitted because they are small, are written in the form

$$0 = f(D + h)v - F \cos(\pi y/b) - Ru - g(D + h)\partial h/\partial x \qquad (1)$$

$$0 = -f(D + h)u - Rv - g(D + h)\partial h/\partial y \quad \ldots\ldots (2)$$

To these, the equation of continuity must be added

$$\partial[(D + h)u]/\partial x + \partial[(D + h)v]/\partial y = 0 \quad \ldots\ldots (3)$$

Cross-differentiation of (1) and (2) and use of (3) results in the following equation

$$v(D + h)(\partial f/\partial y) + (F\pi/b) \sin(\pi y/b) + R(\partial v/\partial x - \partial u/\partial y) = 0 \quad \ldots\ldots (4)$$

In the actual oceans h is so much smaller than D that to a first degree of approximation (4) may be rewritten as

$$\alpha v + \gamma \sin(\pi y/b) + \partial v/\partial x - \partial u/\partial y = 0 \quad \ldots\ldots (5)$$

where the following definitions have been made

$$\alpha = (D/R)(\partial f/\partial y) \qquad \gamma = F\pi/Rb \quad \ldots\ldots (6)$$

To the same degree of approximation the equation of continuity (3) may be replaced by

$$\partial u/\partial x + \partial v/\partial y = 0 \quad \ldots\ldots (7)$$

A stream function ψ is introduced now by the following relations

$$u = \partial\psi/\partial y \qquad v = -\partial\psi/\partial x \quad \ldots\ldots (8)$$

The equation (5) is now rewritten in terms of the stream function

$$\nabla^2\psi + \alpha\partial\psi/\partial x = \gamma \sin(\pi y/b) \quad \ldots\ldots (9)$$

The remainder of this paper is simply a study of solutions of this equation. The boundary conditions upon (9) are that the shore of the ocean be a streamline

$$\psi(0,y) = \psi(\lambda,y) = \psi(x,0) = \psi(x,b) = 0 \quad \ldots\ldots (10)$$

Formal solution of the problem--If f is a linear function of y then α is a constant. Equation (9) is nonhomogeneous and therefore cannot be solved directly by separation of variables. If the right hand member is dropped, the resulting homogeneous equation is soluble by separation. Adding the solution of the homogeneous equation to a particular integral of (9) gives the general solution of (9). A particular integral of (9) is, by inspection

$$-\gamma(b/\pi)^2 \sin(\pi y/b) \quad \ldots\ldots (11)$$

The homogeneous equation is

$$\nabla^2\psi + \alpha\partial\psi/\partial x = 0 \quad \ldots\ldots (12)$$

To solve (9) by separation of variables let ψ be given in the following form

$$\psi = XY \quad \ldots\ldots (13)$$

X is a function of x only, and Y is a function of y only. Equation (9) may therefore be written as the following system

$$Y'' + n^2Y = 0 \quad \ldots\ldots (14)$$

$$X'' + \alpha X' - n^2X = 0 \quad \ldots\ldots (15)$$

The primes represent total differentiation, and n^2 is determined by the conditions (10). The general solutions of these two equations are in series form

$$Y = \Sigma(c_j \sin n_j y + d_j \cos n_j y) \quad \ldots\ldots (16)$$

$$X = \Sigma(p_j e^{A_j x} + q_j e^{B_j x}) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (17)$$

The constants A_j and B_j have been defined thus

$$A_j = -\alpha/2 + \sqrt{\alpha^2/4 + n_j^2}, \text{ and } B_j = -\alpha/2 - \sqrt{\alpha^2/4 + n_j^2}$$

The quantities c_j, d_j, p_j, q_j, are undetermined constants. The general solution of (9) is therefore

$$\psi = XY - \gamma(b/\pi)^2 \sin(\pi y/b) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (18)$$

This solution is very general but reduces to a simple closed form when the boundary conditions (10) are imposed. First of all, the d_j and c_j vanish except c_1 corresponding to $n_1 = \pi/b$. This constant c_1 may be absorbed into p_1 and q_1. Dropping subscripts the stream function now has the form

$$\psi = \gamma(b/\pi)^2 \sin(\pi y/b)[pe^{Ax} + qe^{Bx} - 1] \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (19)$$

where

$$p = (1 - e^{B\lambda})/(e^{A\lambda} - e^{B\lambda}) \text{ and } q = 1 - p \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (20)$$

The curves (ψ = const.) are the streamlines of the ocean currents.

The velocity components u and v may be obtained from (8) by simple differentiation of the stream function

$$u = \gamma(b/\pi)^2 \cos(\pi y/b)(pe^{Ax} + qe^{Bx} - 1) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (21)$$

$$v = -\gamma(b/\pi)^2 \sin(\pi y/b)(pAe^{Ax} + qBe^{Bx}) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (22)$$

The value of h at any point referred to the value of h at the origin may now be obtained by integration of (1) and (2).

$$h(x,y) = -(F/gD)(e^{Ax}p/A + e^{Bx}q/B) - (b/\pi)^2(F/gD)(pAe^{Ax} + qBe^{Bx})[(\cos \pi y/b) - 1]$$
$$- \left\{(f\gamma/g)(b/\pi)^2 \sin(\pi y/b) - (\partial f/\partial y)(\gamma/g)(b/\pi)^3[\cos(\pi y/b) - 1]\right\}\left\{pe^{Ax} + qe^{Bx} - 1\right\} \quad (23)$$

Discussion of the solution for certain ocean systems--In order to clarify the meaning of the foregoing section, it is advisable to see what role the various parameters play by working some numerical examples. Three cases are discussed. All involve the same effects of wind stress, bottom friction, and horizontal pressure gradients caused by variations of surface height. The role of the Coriolis force is different in each case. First it is assumed that the Coriolis parameter vanishes everywhere, the case of the non-rotating ocean. Secondly, it is assumed that the Coriolis parameter is constant everywhere, the case of the uniformly rotating ocean. In the third case it is assumed that the Coriolis parameter is a linear function of latitude. Of the three cases, the last one most nearly approximates the state of affairs in the real ocean.

For convenience of the numerical computations the dimensions of the ocean are taken as follows

$$\lambda = 10^9 \text{ cm} = 10{,}000 \text{ km}$$
$$b = 2\pi \times 10^8 \text{ cm} = 6249 \text{ km}$$
$$D = 2 \times 10^4 \text{ cm} = 200 \text{ m}$$

The maximum wind stress F is taken to be one dyne/cm^2.

The coefficient of friction R is the only quantity for which a value must be devised. If a value of R = 0.02 is assumed, the velocities in the resulting systems approach those observed in nature.

The case of the non-rotating ocean--In this case the constants p and q are particularly simple. Within one per cent, or as closely as graphs may be drawn, p and q are given by

$$p = e^{-\pi\lambda/b} \qquad q = 1$$

The equation for the stream function is therefore

$$\psi = \gamma(b/\pi)^2 \sin(\pi y/b)[e^{(x-\lambda)\pi/b} + e^{-x\pi/b} - 1]$$

The east-west and north-south symmetry of the streamlines is immediately evident from this equation, and the actual streamlines computed from it are exhibited in Figure 2.

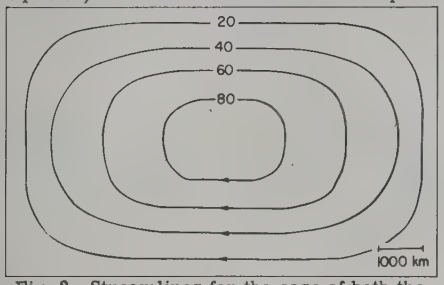

Fig. 2--Streamlines for the case of both the non-rotating and uniformly rotating oceans

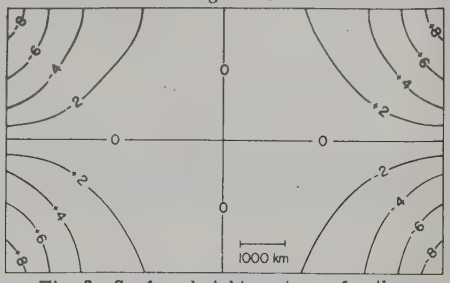

Fig. 3--Surface height contours for the non-rotating ocean in cm

The height contours are computed from (23). Since in this case there is no Coriolis force, the last two terms vanish. Height contours according to this equation are plotted in Figure 3. The general features of the non-rotating wind-driven system are a broad circulation exhibiting absolutely no tendency toward crowding of the streamlines.

The case of the uniformly rotating ocean--In the case where the Coriolis parameter is a constant 0.25×10^{-4}, the streamline diagram does not differ from that of the non-rotating basin. When the height contours are computed however from (23), a difference between the two cases becomes apparent. The third term which vanished in the first case does not vanish in this case. Height contours computed from this equation are exhibited in Figure 4. The large elevation in the central portion of the ocean provides horizontal pressure gradients that largely counterbalance the Coriolis forces. The height contours are not strictly parallel to the streamlines but nearly so.

The case where the Coriolis parameter is a linear function of latitude--In the real ocean the Coriolis force is a function of latitude. In low latitudes this function is nearly a linear one $f = y \times 10^{-13}$. The inequality in the absolute values of the quantities A and B that occurs in this case immediately makes clear the complete lack of east-west symmetry. The streamlines drawn from this formula are shown in Figure 5. The most striking feature of this figure is the intense crowding of stream-

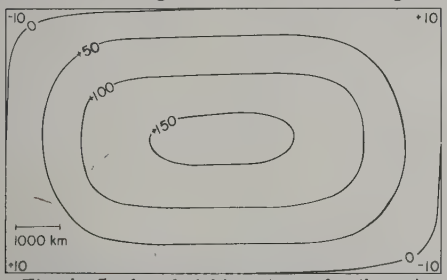

Fig. 4--Surface height contours for the uniformly rotating ocean in cm referred to an arbitrary level

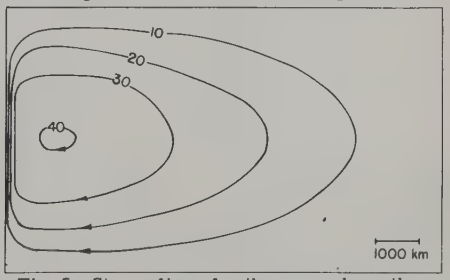

Fig. 5--Streamlines for the case where the Coriolis force is a linear function of latitude

lines toward the western border of the ocean. The rest of the streamline picture is broad and diffuse. The velocity of this system in the region corresponding to the location of the equatorial current (in the actual oceans) is about 20 cm/sec. At the western border the northward velocity amounts to as much as 240 cm/sec. The width of the region of strong northward currents is less than 100 km. The similarity that the velocity field of this simple case bears to that of the actual Gulf Stream suggests that the westward concentration of streamlines in the wind-driven oceanic circulation is a result of the variation of the Coriolis parameter with latitude.

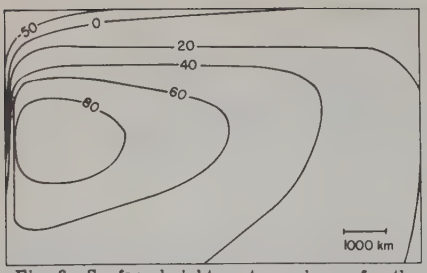

Fig. 6--Surface height contours in cm for the case where the Coriolis parameter is a linear function of latitude

The height contours computed from this case are shown in Figure 6. To extend the results of this study to the Southern Hemisphere the reader will notice that since α is unaffected by crossing the Equator and γ simply changes sign, all the diagrams may be transformed to below the Equator by simple reflection across the x axis. The crowding of streamlines is therefore toward the western border of each ocean, irrespective of hemisphere.

The artificial nature of this theoretical model should be emphasized, particularly the form of dissipative term. The writer thinks of this work as suggestive, certainly not conclusive. The many features of actual ocean structure omitted in the model should be evident.

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(Manuscript received September 25, 1947; presented at the New England Meeting, Woods Hole, Massachusetts, September 18, 1947; open for formal discussion until September 1, 1948.)

Contribution No. 409

Reprinted from SCIENCE, January 2, 1948, Vol. 107, No. 2766, pages 24–25.

A Simple Micromethod for Rapid Extraction of Lipids[1]

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Ever since Soxhlet's (1848–1905) extractor came into general use, many modifications of the fundamental method have been proposed. The problem has been how to extract all the lipids as completely as possible without undue expenditure of time and exposure of the tissue and extract to oxidation. Recently Bloor (*1*) recommended boiling 95% ethanol followed by ethyl ether as the most generally useful solvent in the microdetermination of lipids. The tissue is boiled in an Erlenmeyer flask and the extract separated from the tissue by filtration. Ernst (*2*) uses a sintered-glass plate fused into a separatory funnel for rapid and repeated extraction of fats from meat, combining extraction and filtration into one process. But the method suffers from being a cold extraction only. In the present method the tissue is extracted with boiling solvent, the processes of repeated extraction with fresh solvent and the final filtration are all combined into a single step in the procedure, and the apparatus used can be easily assembled in any laboratory.

The extractor (Fig. 1) consists of a cold finger, A, the end of which is drawn out into a hook and with a bulb blown near the other end in order to rest on and close the mouth of a 100-ml Kjeldahl digestion flask, B. A thin glass rod, C, with a hook on its upper end, is attached on the lower end of the cold finger and leads into a glass tube, E, placed inside an insect vial, D. The inner tube, E, is made from a 6-cm section of ordinary glass delivery tube with a coarse, sintered-glass plate fused onto its bottom. (The sintered-glass plate used here was made by pulverizing a piece of glass tube and fusing the powder onto one end of a 6-cm section of the same material.) The insect vial, D, has a round opening, F, blown out at its lower third.

For microextraction of lipids from tissue the latter is placed in the inner sintered-glass tube, E, which is placed inside the vial, D. The whole is introduced i the Kjeldahl flask with the help of a glass rod while apparatus is in a horizontal position. Ten–20 ml of distilled 95% ethyl alcohol is poured slowly into the fla After clamping the flask and starting the circulation water through the cold finger, the bottom of the flask

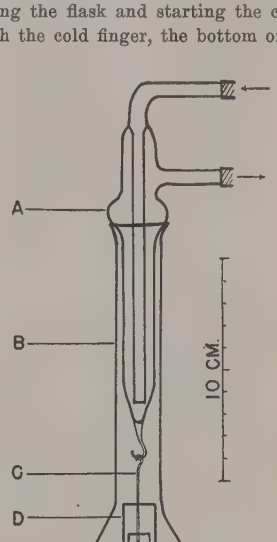

FIG. 1

gently heated with a microflame. As the alcohol bo its vapor is condensed on the cold finger and flows alo the guiding rod, C, into the inner tube, E, and onto tissue which is being boiled at the same time. Condens alcohol will at first accumulate in the inner tube, E, tract the lipids, and be filtered into the outer tube, through the sintered-glass plate. As soon as the alcol in tube D reaches the level of the opening, F, it flows into the flask. In this way the solvent in tube D is ne higher than the level of F, while fresh condensate kee on coming into the inner tube to extract the tissue. Af a specified time the extract is removed from the tu and the flask. A cork mounted on the end of a 25-c long glass rod is convenient for taking the outer tube,

[1] Contribution No. 409 of the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

[2] This work was done at the Marine Biological Laboratory as a part of a research program. I am very grateful to the chairman and members of the Osborn Zoological Laboratory for providing laboratory facilities at Woods Hole.

with its contents, out of the flask. The extraction is completed with ethyl ether in the same way.

In charging the tube with tissue and in removing the extract, precaution is observed against introducing foreign lipids from either the operator's hands or other objects. As some air is always trapped under the vial, D, which then serves as a boiling tube, there is no danger of bumping, for the solvent boils smoothly.

The total extracts recovered after evaporating the solvents under reduced pressure, extracted from different tissues for various length of time (5–20 min), are shown in Table 1. There is apparently no gain in increasing the time of extraction from 10 to 20 min. On the other hand, there seems to be an actual loss in total extract, as shown in the lower half of Table 2, when the time is greatly prolonged. This loss is probably due to the removal of volatile fatty acids during prolonged boiling. Extraction made for 10 min with this apparatus gives very consistent results, as shown in the upper half of Table 2, where the deviation in the four samples is not more than 0.3% from the mean value. For comparison, a piece of the liver from the same tautog was subjected to the classical method of Soxhlet extraction, and the following results were obtained:

TABLE 1

LIPID EXTRACTS FROM DIFFERENT TISSUES OF STARVING *Fundulus heteroclitus* AND *Tautoga onitis*

Tissue	Extraction time (min)	Wet wt. of tissue (mg)	Wt. of extract (mg)	%	Average %	Deviation from average (%)
Brain, *F. heteroclitus*	20	54.1	6.3	11.6	12.6	−1.0
	15	42.8	5.3	12.4		−0.2
	10	29.5	3.8	12.9		+0.3
	5	40.7	5.5	13.5		+0.9
Liver *F. heteroclitus*	20	83.4	13.1	15.7	16.4	−0.7
	15	75.3	12.2	16.2		−0.2
	10	55.3	8.9	16.1		−0.3
	10	46.9	7.7	16.4		0
	5	57.5	10.0	17.4		+1.0
Muscle, *F. heteroclitus*	20	246.6	6.7	2.7	2.8	−0.1
	15	149.5	4.7	3.1		+0.3
	10	173.9	5.1	2.9		+0.1
	5	260.8	6.8	2.6		−0.2
Liver, *Tautoga onitis*	20	130.6	7.3	5.6	5.55	+0.05
	15	92.8	5.0	5.4		−0.15
	10	74.5	4.5	6.0		+0.45
	5	97.7	5.1	5.2		−0.35

TABLE 2

LIPID EXTRACTS FROM FISH LIVER

Tissue	Extraction time (min)	Wet wt. of tissue	Wt. of extract	%	Dev.
Tautog liver	10	275.1	30	10.9	+0.1
	10	238.3	25.8	10.8	0
	10	282.1	29.6	10.5	−0.3
	10	276.9	30	10.8	0
			Average	10.8	
Fundulus liver	10	34.5	7.6	22	
	20	39.0	7.4	19	
	40	46.3	8.5	18.3	
	80	37.9	6.0	16	

Time of extraction in hours	1	2	3	4	5	6
Lipids recovered (%)	4.9	8.0	8.5	9.1	9.5	10.5

Compared with these data from Soxhlet extraction, the results obtained with the present apparatus show that the amount of lipid extracted is not less than the older method, but the saving of time and solvent is obvious.

References

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Contribution No. 410

ZOOLOGY.—*Some interesting starfishes and brittle-stars dredged by the* Atlantis *in the mid-Atlantic.*[1] AUSTIN H. CLARK, U. S. National Museum.

The Woods Hole Oceanographic Institution has recently submitted to me for examination, through Dr. Louis W. Hutchins, a small but interesting collection of starfishes and brittle-stars dredged by the *Atlantis* in the mid-Atlantic. The expedition on which these were found, Cruise No. 150 of the *Atlantis*, was sponsored by the National Geographic Society, Columbia University, and the Woods Hole Oceanographic Institution. I am much indebted to the Institution and to Dr. Hutchins for the privilege of studying this collection.

The species represented in the collection are the following:

Hyphalaster parfaiti E. Perrier

Locality.—*Atlantis* station 15; mid-Atlantic west of Gibraltar (lat. 35° 37′ N., long. 30° 51′ W.); 3,200 meters; August 16, 1947. Seven specimens.

Notes.—The details of the seven specimens are as follows:

[1] Contribution from the Woods Hole Oceanographic Institution No. 410. Published with the permission of the Secretary of the Smithsonian Institution. Received November 5, 1947.

Specimen	R	r	Cribriform organ	United marginals
1	34 mm.	14 mm.	7	10
2	34	13	9	10
3	33	14	5	9
4	30	11	7	8
5	27	11	7	8
6	17	8	7	4
7	17	7	5	4

Pythonaster atlantidis n. sp.

Description.—$R = 165$ mm, $r = 28$ mm. The height at the center of the abactinal system is 26 mm. The rays are 31 mm wide at the base, tapering rapidly to 10 mm at 30 mm from the base, from this point tapering gradually to 3 mm at the tip. A shallow interradial sulcus runs from the middle of each interradius to the center of the disk. The animal may be described as broadly stellate, with each point of the star produced into a long and slender arm.

There is no abactinal skeleton, but the skin is filled with minute rounded plates, which are almost contiguous on the disk and arm bases but become scattered on the outer part of the arms. Among these are the much larger and denser circular lenticular plates, which carry the groups of spines.

On the midline of each ray, running from the center of the disk to the end of the swollen portion of the arm bases, is a band 10–15 mm wide consisting of groups of from 2 or 3 to about 10, commonly 5 or 6, very slender and delicate spines 2–3 mm long arising from a common base on a deeply embedded lenticular plate, the whole enclosed in a bag of thick skin by which the spines are entirely concealed. In a patch about 15 mm long on the inner part of the disk these spine-containing sacculi are intermixed with papulae. On the disk this band of sacculi is bordered on each side by a patch of bare skin through which the large eggs, 2 mm in diameter, are visible. These bare patches may bear two or three sacculi including 4–7 spines. The apical region is closed by 5 large radially placed triangular flaps consisting of numerous delicate spines enclosed in a web of thick skin. The madreporite is situated at the inner end of an interradial sulcus at the outer end of the line between two of these valves or flaps. Just beyond the central valves and bordering the interradial sulcus for about half its length are a few cup-shaped structures consisting of about a dozen slender spines radiating upward from a common base and enclosed in thick skin.

The arms beyond the swollen basal portion are in cross section triangular with the apex rounded, about as high as broad, becoming higher than broad toward the arm tips.

The adambulacral plates have a strongly curved crest which is set at an angle of about 60° with the axis of the arm, the distal end of each crest being considerably farther inward than the proximal end of the crest following. These crests carry a row of 8–10 slender spines which are closely placed with their swollen bases contiguous and are united by a web; the innermost spines are about 1 mm long, those following gradually increasing in length to the outermost, which is 3 mm long. The outer part of each adambulacral plate bears a single much stouter spine 4 mm long, these stouter spines supporting a broad fin-like web which runs along the actinolateral border of the arm resembling the actinal web of many Pterasteridae. Beyond the proximal swollen portion of the arms the adambulacral spines become reduced in number, being usually 5.

Running upward from each adambulacral plate to the dorsolateral border is a band about 1.5 mm broad composed of numerous fine spines arising in small groups, sometimes singly, from a row of independent concretions, the whole band being enclosed in a continuous envelope of thick skin. Beyond the swollen proximal portion of the ray the bands of the two sides meet in the middorsal line. Distally these bands become narrower, the concretions bearing only 1–3 spinelets.

The pair of mouth plates is 9 mm broad at the mouth edge, 2 mm broad on the outer border, and 7 mm long. The line of union of the two plates is raised into a rounded crest. The inner border at the mouth edge is everted and curved, and the outer borders are somewhat concave. The everted inner border of each mouth plate bears 4 large spines, beyond which are 5 much smaller spines. There are no spines on the actinal surface. The mouth plates recall those of some of the Pterasteridae, as for instance *Hymenaster perissonotus*.

The mouth is circular, 23 mm in diameter. The very large stomach is empty. The tube feet, in two series, are large and stout and end in a large sucking disk.

On the arms beyond the swollen basal portion the ambulacral plates are long and slender. The sides of the lower half diverge gradually so that the end adjoining the adambulacrals is

about 2 mm broad, the central portion of the plate being only 0.5 mm wide. The upper third of the ambulacrals is abruptly broadened in the form of a broad Y with very thick arms. When viewed from the exterior the distal arm of the Y is entirely concealed by the proximal arm of the Y of the ambulacral following, which imbricates over it. This causes the ambulacrals when viewed from the exterior, to appear abruptly bent proximally, but when viewed from the interior they are seen to be straight with both arms of the Y about equal.

The adambulacrals as viewed from the actinal edge are seen to be narrowly rhombic, about 3 mm long and 0.75 mm wide. The inner side of the lower angle of the rhombic figure is abruptly swollen, appearing as if a rather thick flat pad had been soldered to it. The distal edge of this pad is evenly curved and bears the spines that form the adambulacral comb. The stout adambulacral spine is situated at about the middle, and widest part, of the adambulacral plate at some distance from the comb-bearing pad and entirely out of line with it. The adambulacral plates are strongly imbricated so that the large spine is in line with the spines of the comb of the plate following, to which it appears to belong unless the arm is cleaned, when its true relationship becomes apparent.

Just above each adambulacral and parallel to its long axis, lying practically on its surface, there is a long, slender and delicate plate 4 or 5 times as long as broad, and a little over half as long as the adambulacral; in some cases there are two of these lying closely side by side. These plates appear to be vestigial marginals.

In a line from these vestigial marginals to the midradial line, as viewed from the inner surface of the skin, there is a regular row of elongate sharply carinate plates 2 or 3 times as long as broad closely placed with their long axes parallel. Between these regular columns of elongate plates (from the center of which on the outer side spines arise) there are very numerous and closely packed minute concretions.

Distally the plates in these columns become smaller, fewer, and more widely spaced, and the concretions become more widely scattered.

Locality.—*Atlantis* station 15; mid-Atlantic west of Gibraltar (lat. 35° 37′ N., long. 30° 51′ W.); 3,200 meters; August 16, 1947. One specimen (type, U.S.N.M. No. E. 7175).

Notes.—The genus *Pythonaster*, the sole genus in the family Pythonasteridae, includes only the type species *Pythonaster murrayi* Sladen described from a single specimen dredged by the *Challenger* at station 323 east of Buenos Aires, Argentina, in 1,900 fathoms, on February 28, 1876.

The type specimen of *P. murrayi* is slightly smaller than the type specimen of *P. atlantidis*, and the bases of the rays are much less swollen; but this difference may be due to the occurrence of large masses of eggs in the type of *B. atlantidis*.

According to Sladen's description and figure the actinolateral areas of *P. murrayi* are traversed by regular rows of isolated skin sacks, whereas in *P. atlantidis* these skin sacks are coalesced into continuous lines. The skin sacks on the abactinal surface of *P. murrayi* are much smaller and more widely separated than those of *P. atlantidis* in which they are almost or quite in contact.

In *P. murrayi* the adambulacral combs are composed of about 6 spines the number becoming reduced to 5 distally. In *P. atlantidis* there are 8–10 proximally, 5 distally. In *P. murrayi* the outermost and largest spine on the adambulacrals is counted as one of the comb, being united to the next by a web. In *P. atlantidis* the outermost spine on the adambulacrals is abruptly larger than the others and relatively much larger than in *P. murrayi* and is joined to the outermost spines on each side by a web, all the spines together and the web forming a continuous broad actinolateral web or fin which appears to be absent in *P. murrayi*.

The mouth plates of *P. murrayi* as figured are not of the same shape as those of *P. atlantidis*. They bear 3 or 4 large inner mouth spines and 3 small outer ones instead of 4 large and 5 small as in *P. atlantidis*. Furthermore, there are in *P. murrayi* spines on the actinal surface of the mouth plates which are not present in *P. atlantidis;* however, in the latter these may have been rubbed off during capture.

With only a single specimen of each species it is impossible to form any idea of the limits of variation. It is possible, though not probable, that *P. atlantidis* is a more fully developed example of the species represented by *P. murrayi*. It is also possible, though not probable, that *P. atlantidis* is a female of the species of which the type of *P. murrayi* is the male; but Sladen did not give the sex of his specimen.

Asteroschema inornatum Koehler

Locality.—Atlantis station 6; mid-Atlantic east of Bermuda (lat. 30° 06′ N., long. 42° 08′ W.), 1,554 meters; August 8, 1947. One specimen.

Notes.—As the original description of this species was brief and lacking in detail the following supplementary information derived from the present specimen may be of interest:

The disk is 6 mm in diameter, stellate with truncated angles and regularly incurved interradial borders; the outer ends of the radial shields are raised about 0.75 mm above the arm bases. The arms are about 60 mm long, slender, 1.3 mm broad at the base and tapering gradually to a delicate tip; they are only slightly higher than broad.

The disk is covered rather thickly with minute granules of coarse and spongy structure. The radial shields are rather broad, widest in the middle, the outer border having a broadly obtuse median angle, and those of each pair are almost in contact. They extend inward for about two-thirds distance to center of disk.

The first two tentacle pores have no scales. The next five have a single tentacle scale. Those following have two scales of which the large inner scale is about a segment and a half in length. At the arm tip the outer scale is only slightly longer than the inner, but neither assumes a hooklike shape. The larger inner scale is cylindrical in the basal third or fourth, from that point being less dense and tapering to the tip. The distal three-fourths bears on the outer side numerous long and slender sharp spinelets, longest near the tip, which through the dried skin appear as small conical points. There are similar but smaller spinelets on the inner side. The small outer scale is similarly armed.

There are 5 stout triangular teeth.

On the sides of the jaw plates within the mouth there are about 8 rather large and well separated granules; these are irregularly scattered, the group as a whole running upward and outward, the outermost being a pair, one on each side of the uppermost tooth.

The skin of the arms contains large delicate filmy plates that appear to form an almost continuous pavement.

The color in alcohol is pale dull pinkish, becoming dark purple on the outer half or more of the tentacle scales.

This species was described by Prof. René Koehler (1907) on the basis of two specimens dredged by the *Talisman* in the Gulf of Gascony (the inner part of the Bay of Biscay) (lat. 45° 59′ N., long. 6° 29′ W.) in 1,480 meters, coral bottom, on August 30, 1883. Sanderson Smith (1888) gives this station as No. 156. Koehler gave the color in alcohol as white.

A single specimen was subsequently dredged by the *Princesse-Alice* at station 2248, in lat. 37° 02′ 30″ N., long. 27° 35′ W., in 1,478 meters, on September 6, 1905 (Koehler, 1909). In his report on the *Princesse-Alice* echinoderms Koehler did not amplify his original description, but he gave a colored figure showing the animal as deep pink, lighter on the radial shields and becoming lighter on the arms after the basal 20 mm.

Ophiura inornata (Lyman)

Locality.—Atlantis station 15; mid-Atlantic west of Gibraltar (lat. 35° 37′ N., long. 30° 51′ W.); 3,200 meters; August 16, 1947. Seven specimens.

Notes.—In these specimens the oral shields are in most divided into two elongate plates meeting in the median line as an angle of about 90°. The jaw plates, the adoral shields, and the two sections of the oral shields are similar, and of about the same size, appearing as three similar chevrons.

In a small specimen one of the oral shields is undivided. In other cases it appears as if the third or outer chevron was composed in reality of a pair of supplementary plates intercalated between the oral shield, much reduced in size, and the adoral shields.

Opiomusium armigerum Lyman

Locality.—Atlantis station 15; mid-Atlantic west of Gibraltar (lat. 35° 37′ N., long. 30° 51′ W.); 3,200 meters; August 16, 1947. Two specimens.

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Contribution No. 411

Reprinted from Biological Bulletin, Vol. 94, No. 1, 25–28, February, 1948
Printed in U. S. A.

THE RESISTANCE OF METALLIC SILVER TO MARINE FOULING

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Copper has been commonly employed to resist the attachment of fouling growths on structures exposed to the sea, while the salts of both copper and mercury are commonly employed as toxic pigments in antifouling paints. The toxicity of solutions of silver salts to organisms such as barnacles has been shown by Clarke (1947) to be comparable to that of copper and mercury. Mr. F. L. LaQue of the International Nickel Company informs us that specimens of fine silver which he exposed at Kure Beach, North Carolina, for as long as 195 days remained practically free of fouling. Similar results were observed by Dr. W. F. Clapp with exposures at Marion, Massachusetts. On the other hand, the Kure Beach specimens when cleaned and re-exposed at Duxbury, Massachusetts, fouled as heavily as nickel or other inert metals tested at the same time. The reason for this difference in behavior is obscure. Mr. LaQue (in press) has classified silver among metals with variable or intermediate ability to resist fouling.

Because of the uncertainty existing concerning the fouling of silver, Mr. LaQue suggested that more systematic tests should be conducted and with the help of Mr. J. L. Christie of the Handy and Harman Company supplied the specimens used in the study to be reported. These consisted of fine silver containing no copper and of coin silver in which 10 per cent of copper is present as an alloy.

In the first experiment, summarized in Table I, two panels of pure silver, one panel of coin silver and one of copper were exposed simultaneously in the sea at Miami Beach, Florida, for one year. One of the silver panels had previously been exposed for two months to running sea water in the laboratory under conditions which permitted a black coating of corrosion products (presumably silver chloride) to form on the surface. The sterling silver and copper panels were 4×6 inches in dimensions, the coin silver 3×3 inches. The panels were held in a wooden frame which prevented metallic contact between them, and left almost the entire area of both sides exposed to the sea water.

Throughout the year's exposure the coin silver remained entirely free of fouling. It resisted attachment better than the sample of copper to which light fouling, consisting of barnacles and encrusting bryozoans, attached temporarily from time to time during the exposure. The copper, however, was entirely clean at the eleventh month, after which the specimen was lost. In contrast, the two specimens of pure silver commenced to foul within the first and second month and both were completely covered at the end of the fourth month of exposure.

One specimen of silver had been soaked in sea water prior to exposure in the sea in the expectation that fouling would be accelerated by the formation of a coating of corrosion products on its surface. This expectation was not realized. The

[1] Contribution No. 411.

TABLE I

Monthly fouling ratings on silver, copper and a silver alloy on marine exposure at Miami Beach, Florida, March 1, 1946–March 1, 1947

Months.....	1	2	3	4	5	6	7	8	9	10	11	12
Silver	3	2	2 1	4	4	4	4	4	4	4	4	4
Silver presoaked 2 months	0	1	2 0	4	4	4	4 3	4	4	4	4	—
Coin silver	0	0	0	0	0	0	0	0	0	0	0	0
Copper	0	0	0	1	1	1	1	0	0	1	0	—

Fouling Ratings

0 = no fouling
1 = <25% fouled
2 = 25–50% fouled
3 = 50–75% fouled
4 = 75–100% fouled

A double rating indicates a different degree of fouling for the two sides of a panel.

panel actually resisted fouling during the early months of exposure better than the specimen immersed with a clean surface of bright metal.

The resistance of copper to fouling was attributed by Sir Humphrey Davy (1824) to the solution of the metal. Subsequent studies (Ketchum, Ferry, Redfield and Burns, 1943) led to the belief that the ions formed on the solution of copper or its salts prevent the attachment of marine organisms by virtue of their poisonous action . Davy's conclusion was based primarily on the observation that copper did not foul when, through contact with a baser metal, a galvanic couple was formed which prevented the solution of the copper. In discussing the germicidal effects of silver, Goetz, Tracy and Goetz (1942) have pointed out that one must distinguish between the volume effect due to small silver ion concentrations in the water and the surface effect which occurs when microorganisms are brought into wetting contact with surfaces on which silver is absorbed. In anticipation of the possibility that metallic silver might resist the attachment of fouling organisms by virtue of some surface effect which would persist after solution was suppressed by galvanic action, a series of silver panels were exposed to the sea coupled with several metals standing higher in the galvanic series.

In this experiment, which is summarized in Table II, strips of copper, nickel, iron, and zinc, 1 × 6 inches in dimensions, were held in contact with 4 × 6 inch silver panels by means of the supporting rack. One uncoupled panel of pure silver was included as a control, as was a silver dollar, as a further check on the fouling of coin silver.

The results confirmed the other experiment in that the silver coin resisted fouling for the entire period of twelve months' exposure except for the temporary attachment of some early larval stages (incipient fouling) during the first two months.

TABLE II

Monthly fouling ratings of silver coupled with various metals on marine exposure at Miami Beach, Florida, January 1, 1946–January 1, 1947

Months....	1	2	3	4	5	6	7	8	9	10	11	12
Ag	1	1	1	1	4*	4*	4*	4*	4*	4*	4*	4*
Ag–Cu	1	1	0	0	4	4	4	4	4	4	4	4
Ag–Ni	2	3	4	4	4	4	4	4	4	4	4	4
Ag–Fe	4	4	4	4	4	4	4	4	4	4	4	4
Ag–Zn	4	4	4	4	4	4	4	4	4	4	4	4
Ag–dollar	½	½	0	0	0	0	0	0	0	0	0	0

* Principally a sponge covering entire panel and excluding other fouling from attaching.

Fouling Ratings

0 = no fouling
½ = incipient fouling
1 = <25% fouled
2 = 25–50% fouled
3 = 50–75% fouled
4 = 75–100% fouled

The pure silver, in contrast, was fouled lightly during the first four months after which it became generally covered with an encrusting sponge.[2]

The effect of coupling the silver to a baser metal was to shorten the time required for the silver to foul. When coupled with the more electro-negative metals, zinc and iron, the silver fouled heavily during the first month. Coupled to nickel the silver showed some slight resistance to fouling only during the first two months. Contact with copper had scarcely any effect on the fouling of the silver. The effects are thus proportional to the difference in potential of the coupled metals.

These results provide a useful control on the resistance of silver to fouling since they show that the light fouling of the uncoupled silver during the early months of exposure are not due to conditions unfavorable to fouling during this period. They warrant the conclusion that the temporary resistance of silver to fouling is dependent on the solution of the metal in the same sense as is the case with copper. There is no indication that the surface of silver, from which solution is prevented by coupling with zinc or iron, has any antifouling action. It should be pointed out, however, that these observations do not preclude in any way the possibility that surface effects such as discussed by Goetz, Tracy and Goetz (1942) might be influential in preventing attachment of fouling if suitable surfaces were established.

The most interesting and perhaps useful result of these experiments is the demonstration of the prolonged resistance to fouling of coin silver, which is apparently equal to copper and superior to pure silver. Coin silver contains about 10 per cent of copper, an amount much less than is present in other copper alloys which successfully resist fouling. The explanation appears to be in the high rate of solution of the coin silver when exposed in the sea.

The specimen of coin silver exposed at Miami lost weight during the year at an average rate of 16.8 mg/dm^2/day, whereas the specimen of pure silver simultane-

[2] Mr. LaQue exposed duplicates of these specimens at Kure Beach, N. C., for 169 days during the summer of 1946. Neither the fine or coin silver showed any fouling. However, fouling at the test location was extremely light.

ously exposed corroded at an average rate of 5.6 mg/dm²/day. Thus, the rate of solution of the silver was three times as great in the case of the coin silver, which in itself may account for its more prolonged resistance to fouling. Moreover, since copper composed 10 per cent of the alloy, copper may be assumed to have been liberated at a rate of 1.68 mg/dm²/day. While this is a lower rate than is adequate to prevent fouling in the case of other copper alloys, it exceeds the rate of solution (1 mg/dm²/day) of copper from effective antifouling paints. It seems probable consequently that the resistance of coin silver to fouling results from the combined effects of the silver and copper ions which are liberated as it dissolves.

A duplicate specimen of coin silver, exposed to the sea at Woods Hole during the same period, lost weight at an average rate of 3.52 mg/dm²/day. This is less than a quarter of the rate of solution observed in the warmer waters at Miami. It seems quite possible that under conditions of exposure which result in such low rates of solution coin silver may foul more readily. Unfortunately, little fouling occurs under any circumstances at the point of exposure at Woods Hole so that this possibility is not tested. Variation in the resistance of specimens of silver to fouling may be expected to result from variations in the conditions of exposure, such as temperature, which influence the rate of corrosion, as well as to variations in the copper present in the alloy.

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Contribution No. 412

Transactions, American Geophysical Union Volume 29, Number 3 June 1948

PROGRESS REPORT ON SCATTERING LAYER OBSERVATIONS IN THE ATLANTIC OCEAN

J. B. Hersey and H. B. Moore

(Contribution No. 412, Woods Hole Oceanographic Institution)

Abstract--Observations with a Fathometer have shown the wide occurrence of a layer of scatterers of supersonic sound in the daytime in the Atlantic Ocean and the Gulf of Mexico at a depth of 150-250 fathoms. Other subsidiary layers are also recorded. The main layer exhibits diurnal migration in depth whose similarity to the behavior of plankton suggests a planktonic control. The behavior of the layer under various conditions, alternative hypotheses on the nature of the scatterers, and preliminary experiments to test the theory of planktonic control are discussed.

Introduction--Observations made by the Division of War Research, University of California in 1942 and 1943, showed that certain of the scatterers of supersonic sound in the ocean are horizontally stratified [UNIVERSITY OF CALIFORNIA, DIVISION OF WAR RESEARCH, 1946]. This was first demonstrated by echo-sounder records of reverberation in sea water which had a structure that could be explained only by postulating one or more layers at depths of 150 to 250 fathoms of some material capable of reflecting supersonic sound. Subsequently this group found that the more prominent scattering layers had considerable diurnal movement, staying at relatively shallow depth in the night and going deeper during the daytime. In September 1946, similar scattering layers were found by the Atlantis during a cruise from Woods Hole to Bermuda. Since that time, scattering layer observations have been carried out by the Atlantis on all her cruises. This report outlines the results obtained so far and discusses briefly some plausible explanations of the phenomenon.

Instrumentation--The Atlantis' Fathometer, which has been used for all routine observations, is keel-mounted and takes soundings by projecting vertically beamed supersonic signals at about 18 kc. A suitable scanning device records the outgoing signal and the returning bottom echo on a slowly moving strip of recording paper so that depth of water under the ship is recorded as a function of time. In usual operation the sensitivity of the receiver is set so as to record only the first echo returning from the bottom. In some places reverberations in sea water are reflected back to the receiver with sufficient intensity to record. This reverberation record generally appears as a faint continuation of the outgoing signal. Schools of fish and various other large masses of organic matter in the water are well known to give a prominent echo return on fathograms.

On September 18, 1946, just north of the Gulf Stream about 150 miles NE of Cape Hatteras, a distinct echo was recorded which became resolved from the outgoing signal five or ten minutes after sunrise and rapidly deepened to about 200 fathoms. It continued at about this depth through the daylight hours and shoaled again about a half hour before sunset. By sunset it was no longer distinguishable from the outgoing signal. Meanwhile, the bottom, which was at about 1500 fathoms, continued to be recorded. On the next day a similar record was obtained. Since that time many such records have been made of the diurnal migration of this scattering layer in different places in the western North Atlantic and in the Gulf of Mexico. Figure 1 shows three typical 24-hour records. The first two are those just described and the other is typical of the Gulf of Mexico.

Figure 2 shows that the scattering layer is definitely not a double-bottom reflection which sometimes may be recorded. It will be observed that on both records there is considerable bottom relief whereas the scattering layer in no way parallels it.

Use of the Fathometer for routine study of this type of phenomenon has the advantage that it records a very large number of signals, thus bringing out any features variable in time or any patchiness in horizontal distribution of the scattering layer. The Fathometer is moderately well suited for statistical study of the behavior of the scattering layer. However, it has several disadvantages: It allows the use of only a relatively narrow range of frequencies; its electrical spark recording feature gives only the crudest sort of data on the intensity of the received sound

and is extremely variable with the condition of the recording stylus and of the recording paper itself; as it is normally operated in deep water, it employs a rather long signal. The signal or ping length measured in equivalent travel distance in sea water is commonly 50 to 90 fathoms. Hence, the received intensity at any given instant is a summation of scattered energy from deep scatterers energized by the first of the signal and shallower scatterers energized by successively later parts of the same signal. This type of scattering record obscures much of the detail and obviously its intensity is not simply related to the density of the scatterers at any given depth. In addition, the first 50 to 90 fathoms of the record are masked by the trace of the outgoing signal.

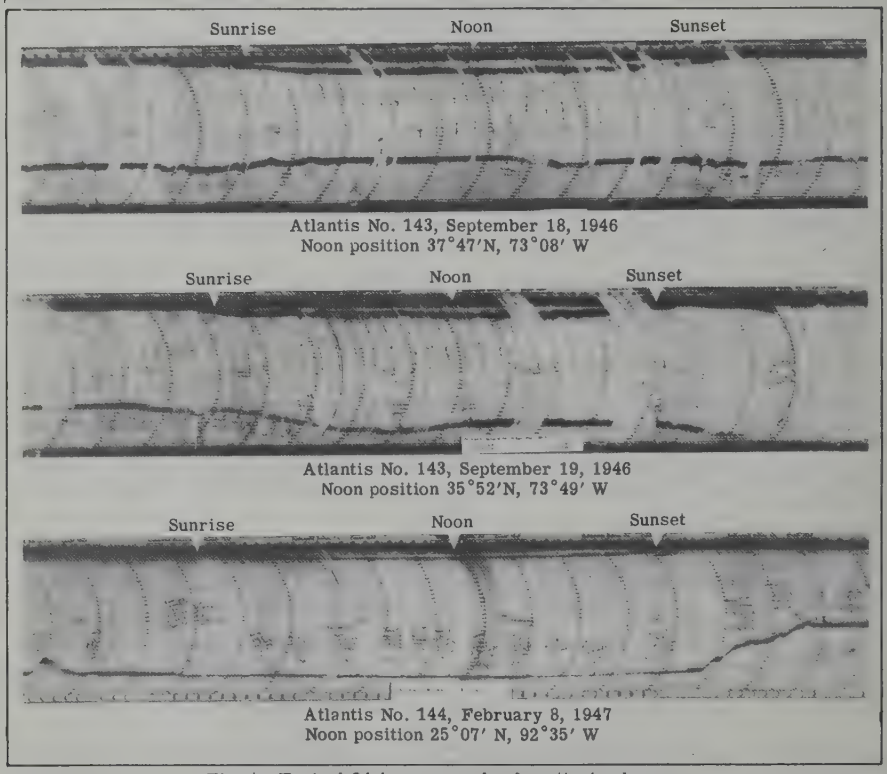

Fig. 1--Typical 24-hour records of scattering layers

By using oscillographic recording to give a faithful picture of the received intensities and a shorter signal to provide more detail, the data have been much improved. The oscillographic recording is done by photographing a cathode ray oscilloscope, connected to the output of the Fathometer's receiver. A set of oscillograms is shown in Figure 3. The oscillograms were taken of several successive signals. Note that no two oscillograms are identical, but all are similar in the general picture of the scattering layers. At the bottom of the figure is shown an oscillogram taken about the same time on the same receiver but using a small explosion as sound source. The depth relations of the peaks of scattering return are closely the same as those above. The signal length for the top oscillograms is of the order of one to three fathoms. The equivalent signal of the explosion is probably of the same order, though it may be somewhat longer.

It has been impracticable to take continuous oscillographic data throughout a cruise. However, the method has been used to study the details of the scattering layer's vertical migration at sunrise and sunset and to take correlation data during net tows. By far the bulk of scattering layer observations have been taken with the conventional Fathometer record at rather long signal lengths. Hence, the effects to be described in the balance of this report are based on this type of data,

excepting only some details of vertical migration to be described later. Plans are now being made for simple recording gear that will provide the quasi-continuous recording of the echo sounder and good reproduction of the received intensities.

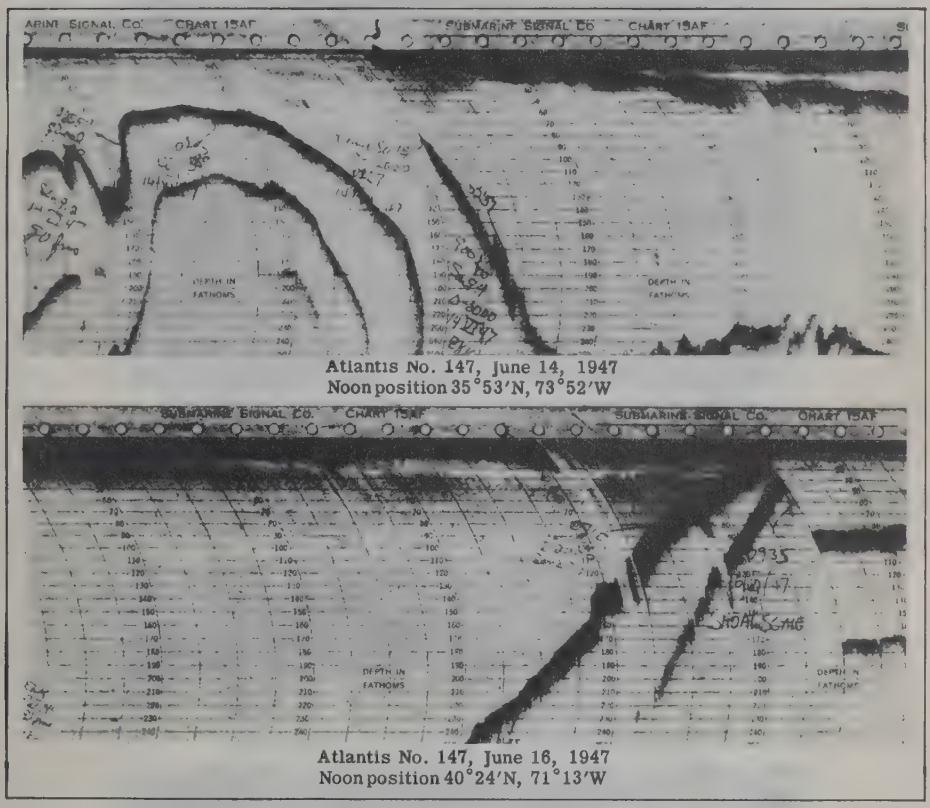
SUBMARINE SIGNAL CO. CHART 15AF
DEPTH IN FATHOMS
Atlantis No. 147, June 14, 1947
Noon position 35°53'N, 73°52'W
SUBMARINE SIGNAL CO. CHART 15AF
DEPTH IN FATHOMS
Atlantis No. 147, June 16, 1947
Noon position 40°24'N, 71°13'W

Fig. 2--Scattering layer over different bottoms

Nearly all data have been taken at about 18 kc. The small amount taken at 24 kc did not differ appreciably. It will, of course, be very interesting to obtain data over a wide range of frequencies since such data should give evidence with regard to the size and nature of the scatterer. The necessary gear is now being prepared and will be used by the Atlantis in deep water soon.

Results--Since September 1946 the Atlantis has covered the area between Woods Hole, Bermuda, and the Antilles and a considerable portion of the Gulf of Mexico in various cruises. Scattering layer observations have been made on upwards of 60 days.

It now appears likely that with varying degrees of definition the main day scattering layer is present universally in deep water throughout the area studied.

The layer has generally been found to be somewhat more diffuse than on the records obtained in September near Hatteras. The types encountered are shown in Figure 4. The first is taken from the early records and looks like a typical bottom echo; the second, which is apparently weaker and more diffuse, is from the Gulf of Mexico; and the third and fourth, which are seen to be very diffuse, are from the Sargasso Sea. These are selected to show the range of definitions encountered but are not necessarily typical of the areas from which they are taken.

Analysis of all the records has been made to determine roughly the depth of the densest concentration of the scatterers at noon. It will be appreciated that in the case of a diffuse layer the

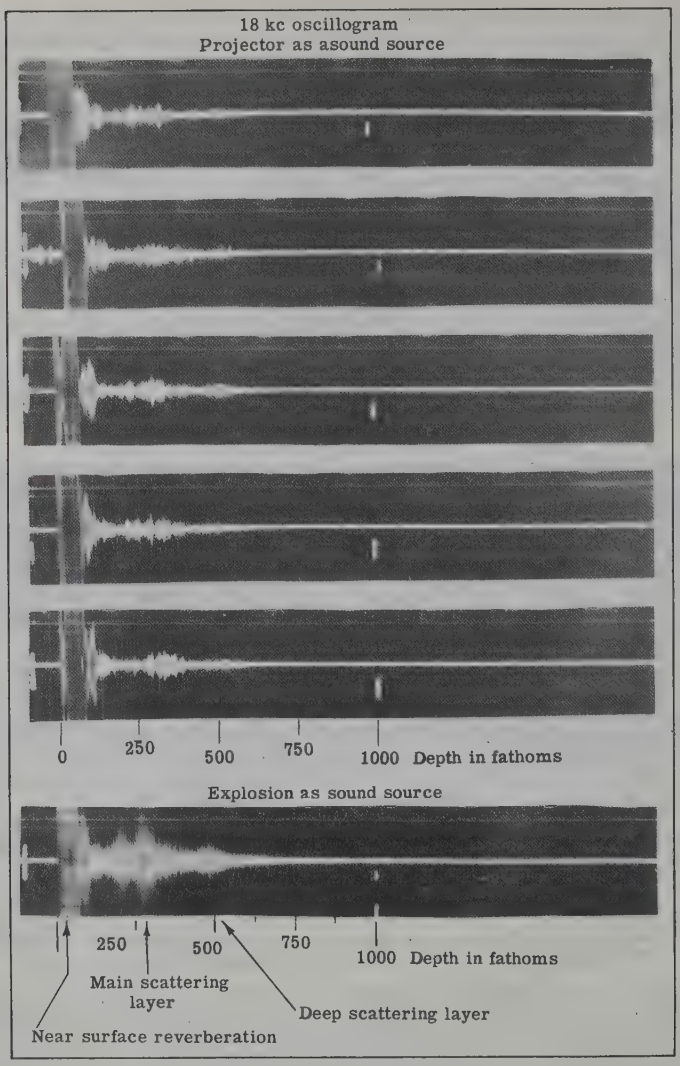

Fig. 3--Oscillograms of scattering layer

recorded sound travel times will not indicate directly the depth of scattering layer since neither its onset nor its deepest limit can be precisely distinguished. Further, the peak of reverberation will not occur precisely at the depth on the record corresponding to the depth of the densest concentration of scatterers in the ocean. This is due in part to the effect of the signal length and in part to divergence of the sound beam from its source. A crude correction has been made for these effects which is easily as good as the echo sounder data warrant. The results in noon depths of scatterers for various locations in the Atlantic and Gulf of Mexico are shown in Figure 5. The circles are noon positions at which observations were taken. The contours show the noon depths of of scatterers over the area. The overall regularity of the contours indicates this is not a random distribution of depth, but a rather regular geographic pattern.

The water at the scattering layer depth was early explored for possible gross effects such as sharp temperature or salinity changes that could reflect sound; no changes were found. This is to be expected since there are no known gross physical effects which have so regular and so large a diurnal change in the ocean. Because of the diurnal movement, the University of California group suggested that the scatterers are living organisms [UNIVERSITY OF CALIFORNIA, DIVISION OF WAR RESEARCH, 1946, p. 7]. This remains the most probable explanation and will be discussed more fully later.

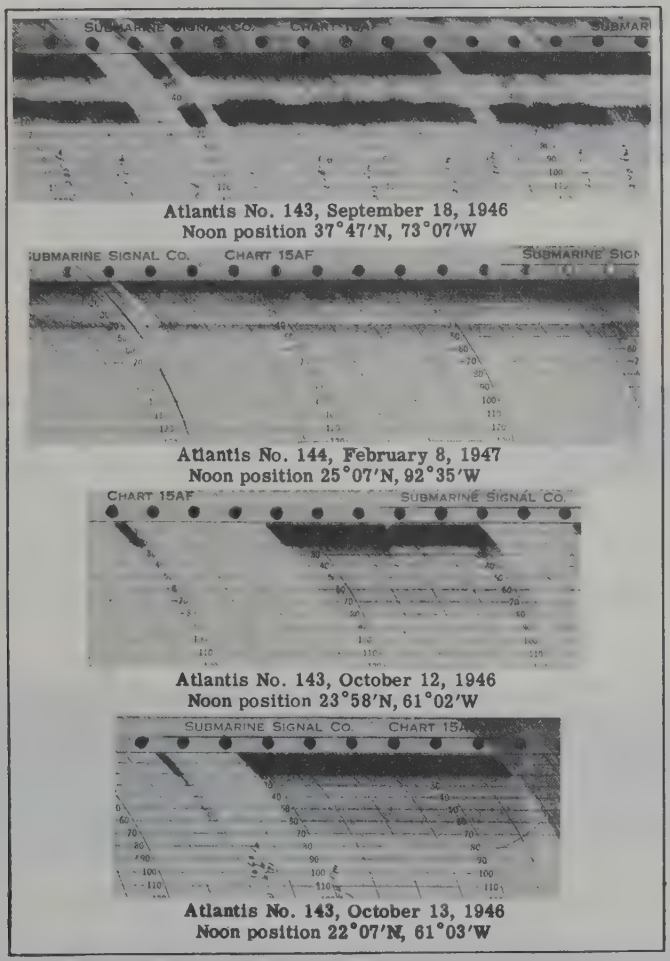
Atlantis No. 143, September 18, 1946
Noon position 37°47'N, 73°07'W
SUBMARINE SIGNAL CO. CHART 15AF
Atlantis No. 144, February 8, 1947
Noon position 25°07'N, 92°35'W
CHART 15AF SUBMARINE SIGNAL CO.
Atlantis No. 143, October 12, 1946
Noon position 23°58'N, 61°02'W
SUBMARINE SIGNAL CO. CHART 15A
Atlantis No. 143, October 13, 1946
Noon position 22°07'N, 61°03'W

Fig. 4--Examples of varying diffuseness of scattering layer

However, before discussing the possible nature of the scatterers it is well to review in greater detail what has been found about their apparent behavior in the Atlantic. First of all we have been referring to "the scattering layer." Actually, in local areas at least, there are several scattering layers and they apparently behave quite differently during any given day. The layer presented, whose depth at noon was mapped in Figure 5, is the most generally observed but there is also in some places a deeper layer that has little or no diurnal movement, and another layer which is generally slightly shallower during the day and apparently moves downward at night. Some of the evidence for these layers is shown in Figure 6. In the upper fathogram the usual layer with its daily vertical motion is evident. Its depth at noon on this day was about 200 fathoms. Another layer is seen at a depth of about 400 fathoms. Its echo is somewhat fainter, probably

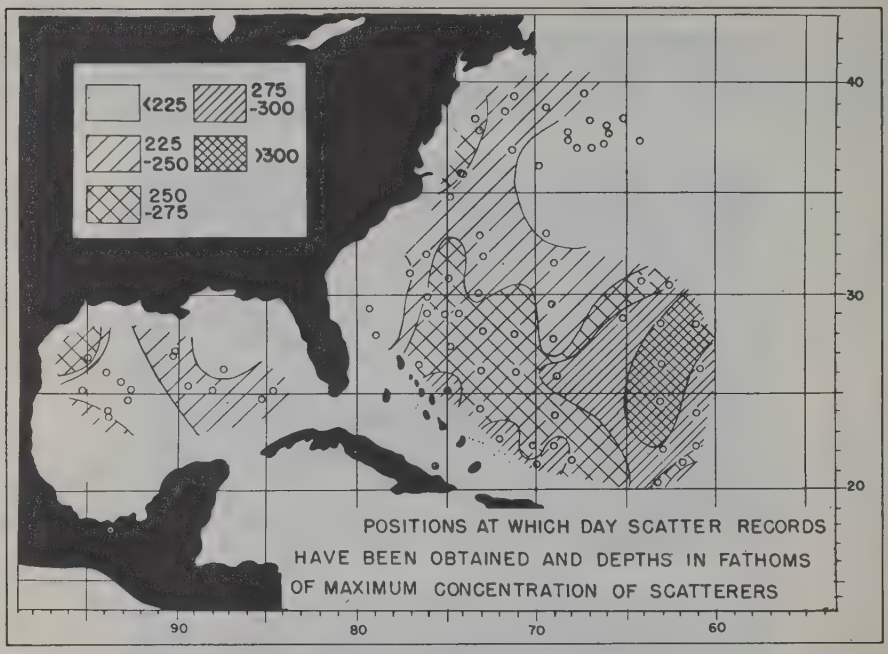

Fig. 5--Scattering layer depths, Gulf of Mexico and western Atlantic

because it is roughly at twice the depth of the other. Evidently this deeper layer, while not stationary, has no pronounced daily movement. Here it migrates downward very gradually about 50 fathoms during the day. In the lower fathogram the usual layer is again shown rising at sunset while another apparently splits off from it and moves downward.

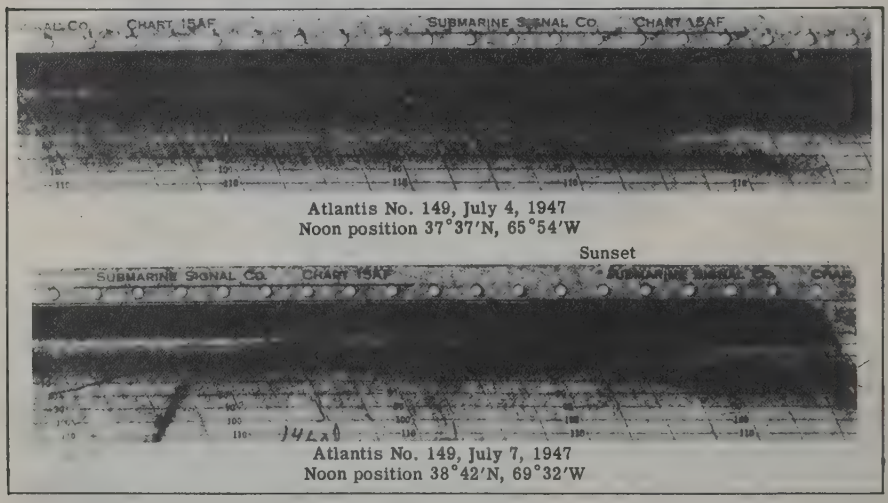
SUBMARINE SIGNAL CO. CHART 15AF
Atlantis No. 149, July 4, 1947
Noon position 37°37'N, 65°54'W
Sunset
SUBMARINE SIGNAL CO. CHART 15AF
Atlantis No. 149, July 7, 1947
Noon position 38°42'N, 69°32'W

Fig. 6--Evening ascent of main scattering layer with other layers showing

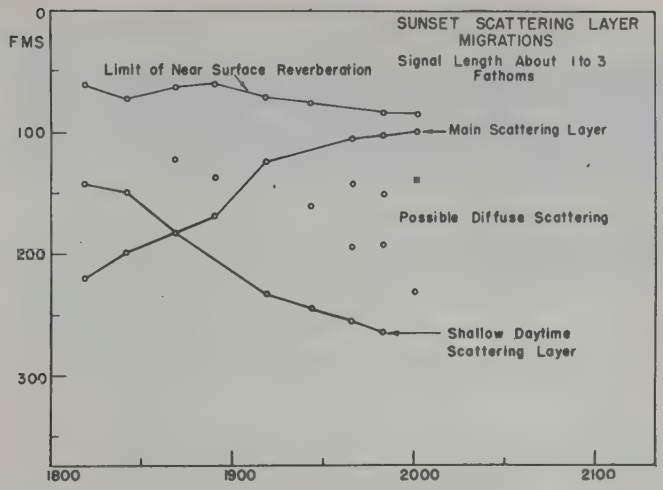

Fig. 7--Analysis of oscillograms taken about sunset, June 1, 1947 at 34°12′N, 73°30′ W

This latter occurrence has been checked by short signal length records taken every ten minutes during a period from about an hour before until an hour after sunset. Analysis of the oscillograms is shown in Figure 7. Here depths of the major peaks of reverberation intensity are plotted as a function of time of day. Of course it is a matter of interpretation whether we say that the shallower layer at 142 fathoms crosses the lower one and goes deep while the deeper one shoals. The interpretation shown is made since it seems to fit more closely the large number of records obtained with long signal lengths. One point of some interest is that the two peaks shown clearly on the short signal oscillograms appear as a single broad peak on the usual Fathometer record. For this reason we have relatively meager evidence for the layer that appears to move downward at sunset. Considerably more data from short signals will be required to determine the extent of its occurrence.

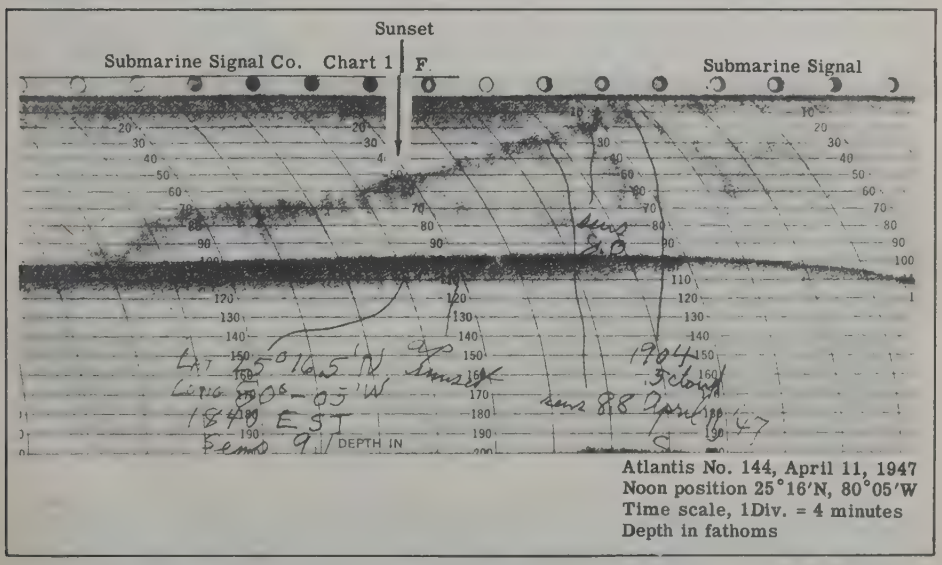

Fig. 8--Sunset ascent of a scattering layer near Miami, Florida, April 11, 1947

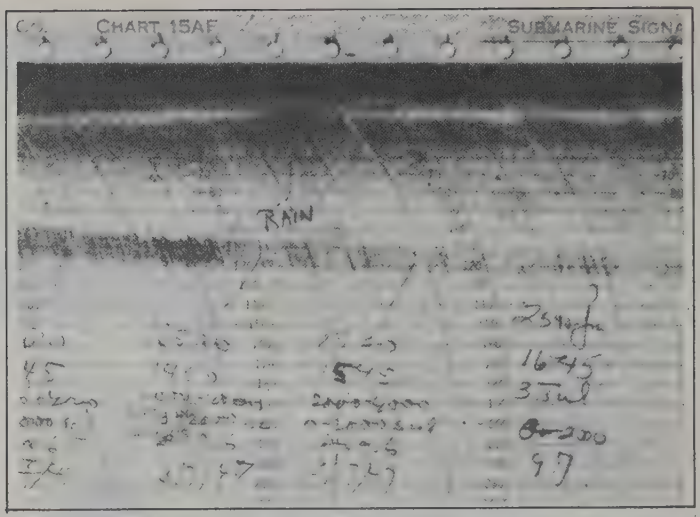

Fig. 9--Effect of heavy cloud on level and diffuseness of scattering layer; Atlantis No. 149, July 3, 1947; noon position 37°26'N, 68°15'W

Whereas the scattering layers have generally been found in water at least several hundred fathoms deep, one very striking record was obtained at sunset on April 11, 1947 in water 100 fathoms deep a few miles southeast of Miami, Florida. This is shown in Figure 8. At about a half hour before sunset a well-defined echo starts to appear just above the bottom and is seen to rise rather steadily to the surface about half an hour after sunset. In the next 20 minutes or so what appears to be the same layer is seen to sink again and become much more diffuse.

Biological correlations--The foregoing facts are the results of direct analysis of records of the Fathometer and other sound-recording instruments. Supposing that the scatterers are living organisms capable of diurnal migration let us consider the correlation of scattering layer behavior with certain factors known to influence plankton behavior. Of these, illumination and temperature are known to be particularly significant. Salinity variations are considered to be of negligible influence in the area under consideration. Temperature data are available from concurrent hydrographic observations.

The most commonly recorded scattering layer is apparently strongly affected by illumination in the water, as shown by the striking diurnal depth variation and by the effect of local heavy cloud cover. Figure 9 shows a record obtained while the Atlantis was passing through a particularly heavy rain squall. The effect of illumination has been analysed somewhat more closely by determining the depths of the recorded maximum return as a function of local apparent time and plotting these on a reference grid of illumination as a function of depth and time. Typical plots are shown in Figure 10. The illumination grid is somewhat arbitrary; it was constructed making proper allowance for Sun's altitude and the absorption coefficient for sea water in the locality. No allowance was made for variations in cloud cover or state of sea.

The illumination curves are not intended to be exact but rather to indicate the trend of diurnal variations in depth-light distribution. They are spaced 100-fold apart. These plots have proved instructive in demonstrating that the scattering layer follows the trend of the contours of equal illumination during times of rapidly changing illumination. However, during the middle of the day, a distinct flattening of the scattering layer curve occurs which suggested that some effect other than illumination might act as a barrier to further downward motion. Low temperature is proposed as a likely barrier.

That temperature changes do act as barriers was demonstrated in a number of observations taken while the Atlantis was crossing and re-crossing the edge of the Gulf Stream. Figure 11 shows such an instance. Gulf Stream water was entered from the northern side and a short time later the ship zig-zagged out of the Stream again. The fathogram shows a diffusing and deepening

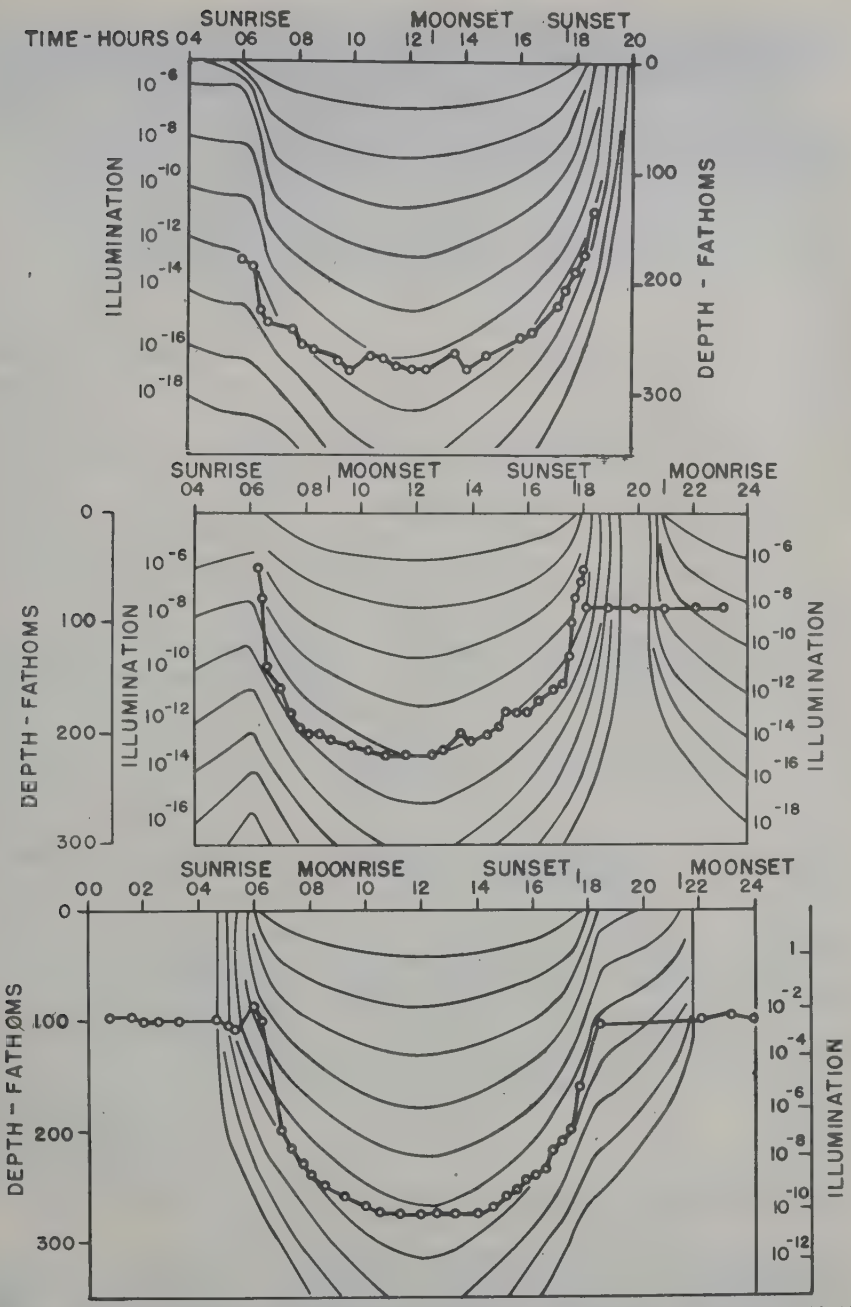

Fig. 10--(a) Diurnal variation in level of scatter return and of illumination on September 18, 1946; noon position 37°47'N, 73°08'W; (b) diurnal variation in level of scatter return and of illumination on February 8, 1947, noon position 25°07'N, 92°35'W; (c) diurnal variation in level of scatter return and of illumination on February 24, 1947, noon position 25° 26'N, 93°44'W

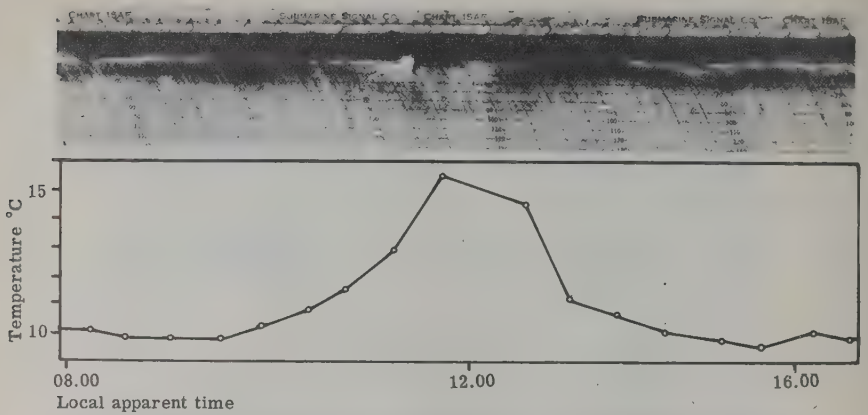

Fig. 11--Fathometer record and temperature profile at 135 fathoms; Atlantis No. 149, July 1, 1947; noon position 36°59'N, 66°57'W

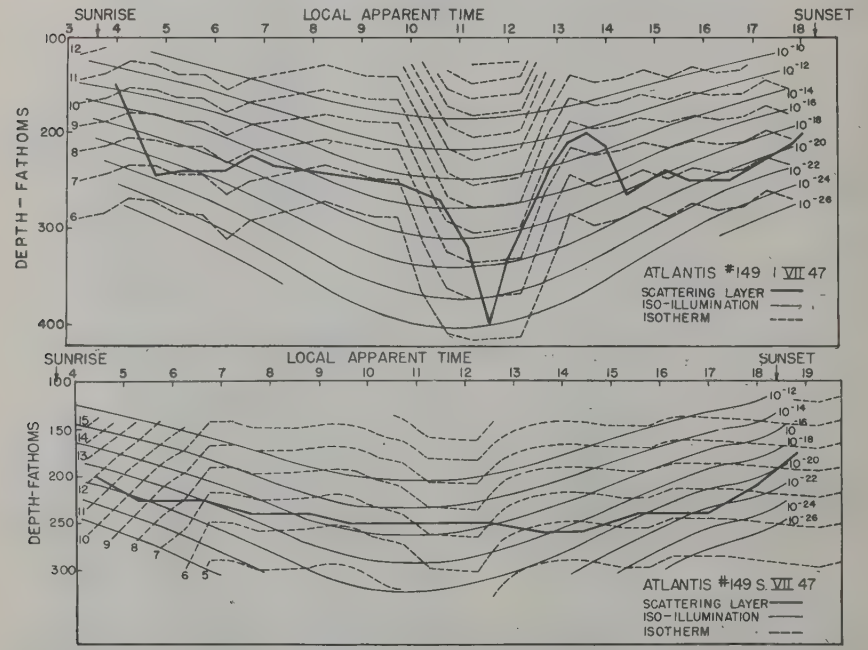

Fig. 12--Temperature, illumination, and scattering layer (a) on crossing and recrossing edge of Gulf Stream; (b) on a day entirely in colder water

of the scattering layer while in Gulf Stream water. In Figure 12a the depth of the scattering layer is superimposed on an illumination grid and temperature profile. The abrupt change in depth on entering and leaving the warm water is clearly shown. For comparison a similar record is shown in Figure 12b for a day in which the ship remained in the colder water throughout the midday period.

Figure 13 shows a record from a similar zig-zag in and out of the Gulf Stream in which the scatterer apparently disappears in the warm water and at the transition points there appears to be a greater concentration of scatterers than in adjoining cold water. An adequate explanation of this behavior must await more general knowledge of the nature of the scatterer.

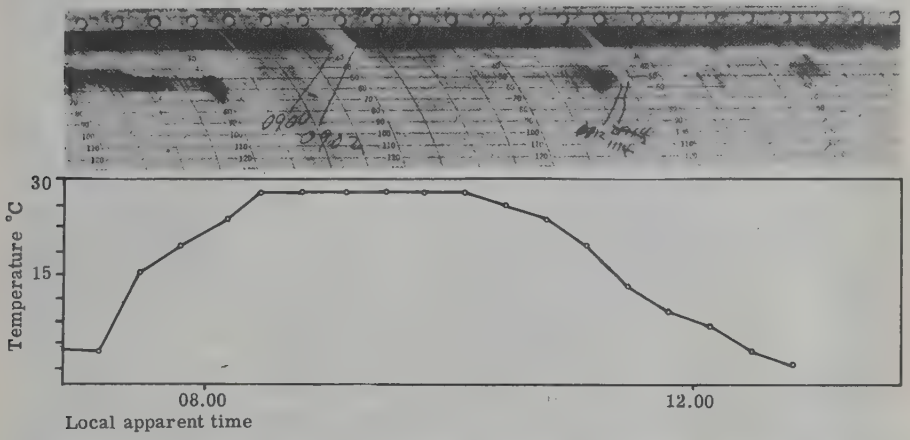

Fig. 13--Fathometer record and temperature profile at 80 fathoms; Atlantis No. 147; June 14, 1947; noon position 35°53'N, 73°52'W

Since no known physical agency could account for the characteristics which we have recorded for the scattering layer behavior, it remains to be seen to what extent a known biological agency could meet the case. Many planktonic organisms are known which exhibit a diurnal migration of the type found in the main scattering layer. A number of groups of plankton animals can be eliminated as improbable on account of their gelatinous consistency, very small size, or differing vertical distribution. Euphausid shrimps seem at present to meet the requirements best. These have a chitinised carapace. They are about an inch long, which corresponds approximately with a quarter of the wave length of sound in use on the Fathometer. They occupy the required day and night

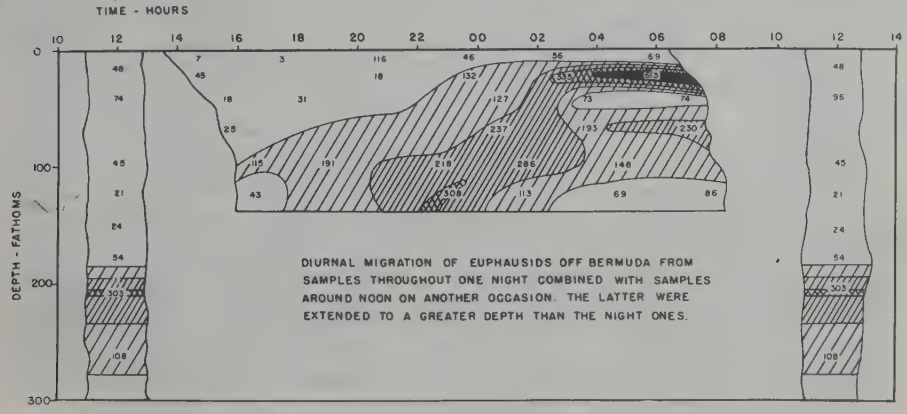
TIME - HOURS
10 12 14 16 18 20 22 00 02 04 06 08 10 12 14
0
100
200
300
DEPTH - FATHOMS
DIURNAL MIGRATION OF EUPHAUSIDS OFF BERMUDA FROM SAMPLES THROUGHOUT ONE NIGHT COMBINED WITH SAMPLES AROUND NOON ON ANOTHER OCCASION. THE LATTER WERE EXTENDED TO A GREATER DEPTH THAN THE NIGHT ONES.

Fig. 14--Diurnal migration of euphausids off Bermuda

levels as shown in Figure 14, which gives the results of a series of net hauls made near Bermuda. It should be noted that the requirements of the sampling methods have resulted in a considerable smoothing of the curves of ascent and descent in this diagram, whereas a much truer picture is obtained from the instantaneous records of the fathograms. Figure 15 shows similar results obtained further west [WATERMAN, NUNNEMACHER, CHASE and CLARKE, 1939] and includes in addition some other plankton crustacea, but gives a similar overall picture. During the course of

the present work we have, whenever possible, taken net hauls at the level indicated by the fathograms for the maximum concentration of scatterers as well as above and below this. Figure 16 shows two such hauls, one in and one above this maximum level and demonstrates clearly the concentration of euphausid shrimps in the former.

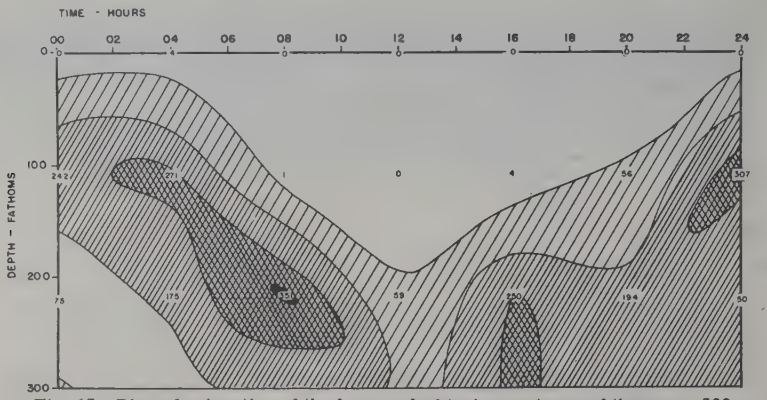

Fig. 15--Diurnal migration of the larger planktonic crustacea of the upper 300 fathoms modified from Waterman, Nunnemacher, Chase and Clarke, 1939: 39°N, 70 1/2°W

That euphausids are present in sufficient numbers is indicated by calculations made from these and other net hauls. From them it appears that a beam of sound projected from the surface to the depth of the scattering layer would suffer at least one to five per cent interception by euphausids, and probably considerably more.

From the point of view of correlation with known behavior and population density then, euphausids appear an adequate explanation of the scattering layer. As already mentioned, though, the problem is a very complicated one. Such a record as that shown already (see Fig. 8) off Miami could be taken as an ideal diagram of the evening ascent of plankton, followed immediately after sunset by sinking and diffusion. The complex behavior of the subsidiary scattering layers indicated by the short ping length records is in agreement with the fact that, at least in the Bermuda area, there is one dominant euphausid, Euphausia brevis, together with smaller numbers of other species, each with its particular vertical distribution and diurnal migration pattern. Some plankton forms even are known which appear to show a descent at night. Clearly, until our knowledge of the details of both the various components of the scattering layers, and the plankton themselves, are considerably advanced, our explanations must not be taken as more than tentative.

One serious difficulty with the hypothesis that the euphausids themselves scatter sound is their small size and the absence of any sort of swim bladder or other associated air bubble to reflect sound. The hypothesis has been advanced that possibly the scatterers are not the euphausids but fish that may be feeding on them and hence concentrating at their level. Little is known of fish populations in deep water because of the difficulty of catching them in net tows. The fish hypothesis is somewhat more attractive from the physical point of view in explaining the intensity of scatter return. If it proves to be the more promising hypothesis after more quantitative studies have been made our ideas about the size and distribution of fish populations in the main oceanic basins will have to be considerably altered.

At present, adequate data do not exist on the acoustic properties of plankton to decide between the two hypotheses outlined above. A controlled series of tests using small crustacea as sound scatterers is now underway, which, with adequate absolute sound measurements of the deep scattering layer, can be expected to clarify the nature of the scattering.

Preliminary observations have demonstrated that shrimps in moderately large quantity (of the order of 100 individuals in the sound beam at once) will reflect sound at about 20 kc at ranges of the order of six to eight feet from the projector receiver. Reasonable precautions were taken to assure that no foreign matter such as sand grains were with the shrimp and that no air bubbles stuck to them. No observations have been made at other frequencies nor has any calibration been

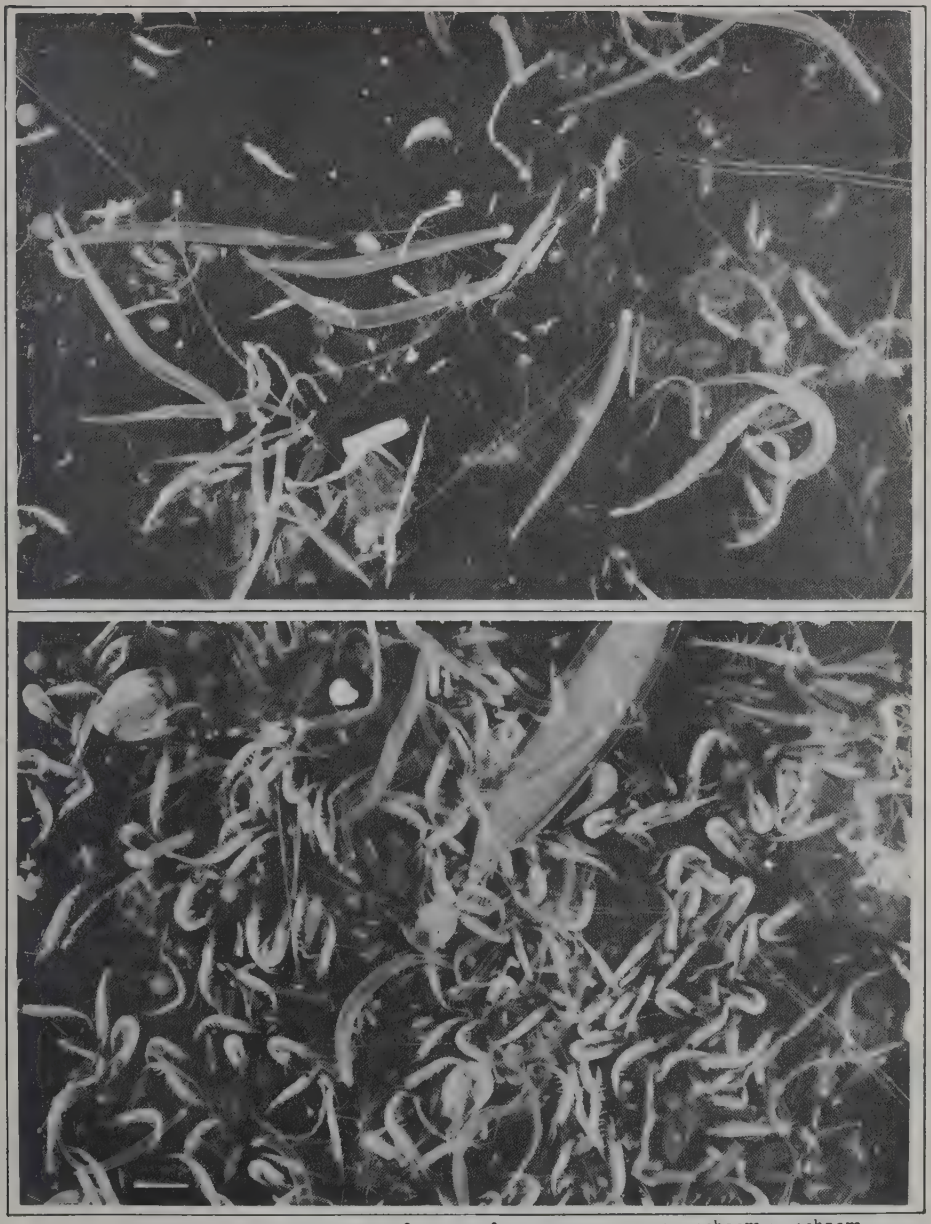

Fig. 16--Simultaneous net hauls at 29°57'N, 75°59'W; June 10, 1947; 16^h20^m to 16^h50^m L. A. T. (a) above scattering layer, 175 fathoms; (b) in scattering layer, 220 fathoms

made of the echo strength in these tests. When more quantitative tests have been made under suitably controlled conditions it will be possible to decide whether shrimp echoes can possibly account for the scattering layer data. Further controlled tests will include studies of various planktonic forms over a wide range of frequencies.

Contribution No. 416

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VOL. VI NO. 1 EXPERIMENTAL STRESS ANALYSIS

THE COLLAPSE OF LONG CYLINDRICAL SHELLS* UNDER EXTERNAL PRESSURE

SIDNEY CORNELL, Massachusetts Institute of Technology

Scope and Object of this Report

The studies on which this paper is based were made primarily to supply a working theory for the design of Woods Hole pressure detonators. These detonators, invented by Dr. Maurice Ewing and Mr. J. Lamar Worzel of the Woods Hole Oceanographic Institution, are made for the purpose of firing explosive charges at depths of from 100 to 1000 fathoms below the surface of the sea. They are actuated by the collapse from elastic instability of cylindrical shells under axial and radial hydrostatic pressure. Cylindrical shells suitable for this purpose have relatively high length over diameter ratios.

While some studies have been made in the range applicable to the detonator problems, the principal literature on the collapse of cylindrical shells has dealt primarily with, first, the development of general equations, as the equation of R. von Mises[1]†, which prove to be too complex for facile application in design; second, the derivation of approximate formulas, as the formula of Windenburg and Trilling[2], suitable for use in design but involving relatively short cylindrical shells; and third, the derivation of equations applicable to infinitely long cylindrical shells, as the equation of Bresse[3] and Bryan[4].

It is the object of this paper to show the development of a formula similar in application to that of Windenburg and Trilling but covering larger length-diameter ratios, and to correlate this formula with observed data.

The experimental work was performed at the Woods Hole Oceanographic Institution from January to March 1947 by the author in connection with the long-range sound transmission project under the direction of Dr. G. P. Woollard.

* The investigation described in this report was carried out when the writer was affiliated with the Woods Hole Oceanographic Institution at Woods Hole, Mass.

† Superiors in parentheses refer to bibliography at end of paper.

Method of Obtaining Data

Two hundred and fifty-eight specimens of various free lengths and wall thicknesses were tested. All specimens were made from high brass tubing (.003 hard temper) with an inside diameter of .250″. Overall lengths of the tubes used were 1½″, 2″, 2½″, 3″ and 3½″. Ends of the tubes were closed with a brass cap at each end and sealed with lacquer as shown in Fig. 1. One exception is to be noted, however, in regard to the method of sealing the ends of the tubes. The tubing of .0075″ nominal wall thickness (except those of 1½″ free length) had a cap sealed with lacquer at one end and a cap sealed with solder at the other. The caps projected into the tubes 1/16″, making the free length 1/8″ shorter than the overall length of the tube. Wall thicknesses of .005″, .006″, .0075″, .008″, .0095″, and .0125″ were called for and the manufacturer supplied the material within a few ten thousandths of an inch of these figures, as will be described.

The shells were subjected to external water pressure by means of simple pressure vessel-pump system. The pressure was measured by means of a special bourdon type gage. The accuracy of the gage was within ½% of the reading from 600 psi to 3000 psi. Below 600 psi the readings were accurate within 3 psi. Calibration was performed by the use of a 500-lb Crosby and a 10,000-lb American Instrument Co. gage testers. As considerable shock was experienced on the collapse of the test specimens, a choke coil consisting of 50 feet of 1/8″ copper tubing and 50 feet of 3/16″ copper tubing in series was used to reduce the possibility of damage to the instrument. The limit of the range of the gage was 3000 psi. As the collapsing pressures for the .0125″ wall thickness specimens were in the neighborhood of 4000 psi, a standard 5000-lb pressure gage was used in that range. An approximate calibration of this gage was obtained by extrapolation from a comparison with the 3000-lb gage.

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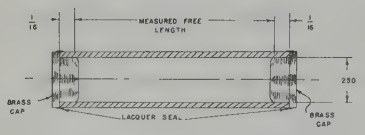

FIG. 1. Schematic diagram of test specimen.

Observed values were tabulated and median values obtained except for the three shortest lengths in the .0125″ wall thickness specimens for which only two observations each were made. Median values, interquartile range, and number of test specimens are given in Table I. Fig. 2 shows a series of test specimens of varying lengths before and after collapse.

The wall thickness of each test specimen was checked roughly by measuring the outside diameter with micrometers and then computing on the basis of an inside diameter of .2500″. It will be shown later in the paper that for a diameter of the neutral axis in the neighborhood of .250″, variations of as little as .0001″ in wall thickness are of importance. It was not practical to measure all specimens to that degree of accuracy. However, representative samples were selected. These were sawed along the axis into four quarters. Each quarter was then measured on a supermicrometer, using a .15605″ diameter ball to contact the concave surface. The contact pressure was 2½ lb. Results were checked with an electrolimit gage and the readings by either method were found to agree within .00005″. These measurements were made by Mr. Arthur Cox of Pratt and Whitney Aircraft. Observed values are tabulated with other data in Table II.

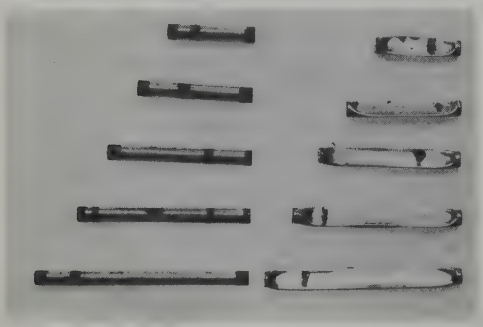

FIG. 2. Test specimens before and after collapse.

Development of Formula

The general equation of von Mises[1] for the collapse of cylindrical shells under external axial and radial pressure may be written:

$$p = \left[\frac{1}{3}\left\{\left[n^2 + \left(\frac{\pi D}{2L}\right)^2\right]^2 - 2\mu_1 n^2 + \mu_2\right\}\frac{2E}{1-\mu^2}\left(\frac{t}{D}\right)^3 + \frac{2E\,(t/D)}{\left[n^2\left(\frac{2L}{\pi D}\right)^2 + 1\right]^2}\right] \cdot \frac{1}{n^2 - 1 + \frac{1}{2}\left(\frac{\pi D}{2L}\right)^2}, \quad (1)$$

$$2\mu_1 = \left[1 - (1+\mu)\,\rho\right]\left[2 + (1-\mu)\,\rho\right],$$

$$\mu_2 = (1+\rho\mu)\left[1 + (1+2\mu)\,\rho - (1-\mu^2)\left(1 + \frac{1+\mu}{1-\mu}\rho\right)\rho^2\right],$$

$$\rho = \frac{1}{n^2\left(\frac{2L}{\pi D}\right)^2 + 1}.$$

where:

p = failing pressure
n = number of nodes in which the tube fails
D = diameter to neutral axis
L = free length
t = wall thickness
μ = Poisson's ratio
E = Young's modulus

The number of nodes, n, in which the shells will fail may be determined by trial from Eq. (1). n is established as the integer giving a minimum value of p. For values of t/D greater than .010 and L/D greater than 5, n has a value of 2. In these experiments the minimum value of t/D was .020 and the minimum value of L/D was 5.52, which is well within the range for n equal to 2. All test specimens were observed to fail in two nodes, confirming the prediction from Eq. (1).

Because of the relatively large values of L/D, certain approximations can be made in Eq. (1). With a value of n equal to 2, the resulting approximate relation is:

$$p = \frac{2E}{1-\mu^2}\left(\frac{t}{D}\right)^3 + .253E\,\frac{tD^3}{L^4}. \quad (2)$$

An interesting comparison is to be had with the equation for cylindrical shells of infinite length as given by Bresse[3] and Bryan[4], which may be written:

$$p = \frac{2E}{1-\mu^2}\left(\frac{t}{D}\right)^3. \quad (3)$$

TABLE I

FAILING PRESSURES OF TEST SPECIMENS IN PSI

Nominal wall thickness (inches)		Overall Length (inches)				
		1½	2	2½	3	3½
.005	Failing pressure	461	328	291	271	268
	Interquartile range	20	22	11	17	14
	No. specimens	12	12	12	8	8
.006	Failing pressure	825	633	556	533	532
	Interquartile range	11	16	7	15	5
	No. specimens	8	8	8	8	8
.0075	Failing pressure	1310	1080	1020	1022	....
	Interquartile range	68	52	54	48	....
	No. specimens	12	12	8	8	....
.008	Failing pressure	1356	1150	1083	1050	1038
	Interquartile range	43	76	25	19	33
	No. specimens	12	12	12	8	8
.0095	Failing pressure	1948	1734	1695	1643	1688
	Interquartile range	65	15	62	39	35
	No. specimens	12	12	12	8	8
.0125	Failing pressure	4025* 4085*	3715* 3825*	3435* 3715*	3587	3550
	Interquartile range	....	....	....	120	60
	No. specimens	2	2	2	8	8

* Observed Values

TABLE II

WALL THICKNESS IN INCHES

Nominal value t	Best experimental value (Figure 3) t	Measured values of t
.0050	.0051	.0049 — .0050 — .0051 — .0052
.0060	.0065	
.0075	.0079	.0077 — .0077 — .0080 — .0080
.0080	.0081	
.0090	.0094	.0096 — .0097 — .0098 — .0098
.0120	.0121	.0120 — .0123 — .0130 — .0131

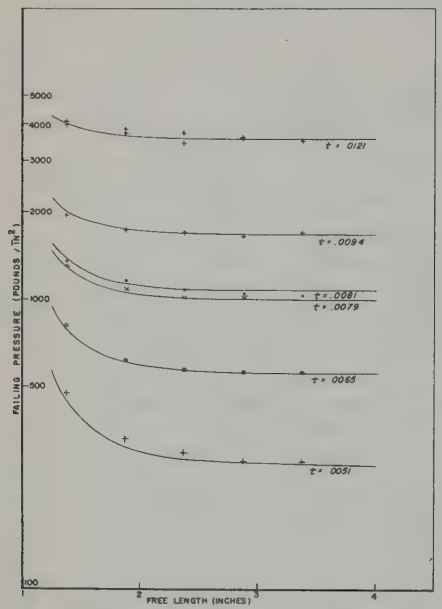

FIG. 3. Failing pressure vs free length for various wall thicknesses.

For hard high brass tubing as used in these experiments, $E = 14 \times 10^6$ lb/in^2 and $\mu = .333$. The inside diameter of the tubing was in all cases .250 and this is assumed to be equal to the diameter of the neutral axis. Hence, for this particular study Eq. (2) becomes:

$$p = 2.01 \cdot 10^6 \cdot t^3 + 55{,}400 \frac{t}{L^4}. \qquad (4)$$

Correlation of Observed Data with the Approximate Formula

In Fig. 3 are plotted median values of the failing pressure for cylindrical shells of various wall thicknesses against free length. (For the three shortest lengths on the .0125 tubing, observed values are plotted.) In attempting to correlate values from Eq. (4) for appropriate wall thicknesses, it was found that the effective free length differed from the measured free length by approximately .27", so that the formula for failing pressure as plotted in Fig. 3 becomes:

$$p = 2.01 \cdot 10^6 \cdot t^3 + 55{,}400 \frac{t}{(L - .27)^4}. \qquad (5)$$

It is probable that the brass plugs inserted 1/16" into the ends of the tubes offer a restraint that reduces the effective free length. No particular difference is to be detected in the effect of soldered-in plugs as compared with lacquer-sealed plugs, although the solder was well "sweated" into the joint and the lacquer applied only to the external seam.

CONCLUSION

The general effect of end constraint on effective free length is worthy of further study. This would involve evaluating k under various conditions in the following generalization of Eq. (5):

$$p = \frac{2E}{1 - \mu^2}\left(\frac{t}{D}\right)^3 + .253E \frac{tD^3}{(L - k)^4}. \qquad (6)$$

where k is the reduction in effective free length from measured free length for a particular condition of end constraint.

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"Contribution No. 416 from the Woods Hole Oceanographic Institution"

PRINTED IN U. S. A.

Contribution No. 417

(*Reprinted from* NATURE, *Vol.* 161, *page* 602, *April* 17, 1948.)

The Swimming of Dolphins*

DOLPHINS in the Gulf of Panama have been seen moving through the sea at a speed of ten knots, their entire bodies showing no apparent swimming motion. This performance was confined, in my observations, to the area immediately forward of the stem (prow) of a sea-going tug and to an estimated depth of one metre or less. Elsewhere near the bow, vertical oscillations of dolphins' tails were readily timed with a stop watch.

When this 'motionless' swimming was first noticed, the animals were in the normal swimming position. In this position it was difficult to be sure that vertical motions of their tail surfaces were not occurring, since the direction of such motions would be nearly parallel with the line of sight of the observer. However, on several occasions dolphins were seen to turn on their sides during the 'motionless' swimming in such a position that their usual swimming motions would have been normal to the line of sight. No motion was visible in these animals, which were clearly seen just below the surface of the water. One animal remained on its side in this manner for 59 sec., which represented a distance, at 5·15 m./sec. (10 knots), of 304 metres. At this time dolphins swimming near by used 1·9 tail oscillations per second in keeping pace with the vessel.

These 'motionless' dolphins seemed to be riding the bow wave (that is, falling down the inclined surface). However, if dolphins are equal in weight to the weight of the water they displace, wave riding is not possible. No data have been found concerning their density. Kellogg[1] says, however, that dolphins usually sink when shot. Is it possible that they are dense enough to fall down the advancing slope of the bow wave, having achieved terminal velocity initially by swimming? A low over-all resistance to motion through the water would seem to be required. Gray[2] has indicated that the work done by dolphin muscle in producing a speed of 10 m./sec. is comparable to the work of other mammalian muscle tissue, if laminar flow is assumed around the dolphin. With turbulent flow, Gray found that the work done by dolphin muscle at 10 m./sec. would be about seven times the

* Contribution No. 417 of the Woods Hole Oceanographic Institution.

work of other mammalian muscle. If a laminar regime exists at a speed of 5 m./sec., perhaps the over-all resistance to the motion of a dolphin is low enough to allow an animal, of sufficient negative buoyancy, to fall down the inclined water surface of a bow wave or other waves.

It may be thought that the dolphins were gaining a forward thrust by placing their tails against the ship's stem. Dolphins have been seen with their tails in momentary contact with the hull, but in the above observations of 'motionless' swimming the animals were clearly forward of the vessel.

Shoulejkin[3] suggests that the speed of motion of the dolphin's tail may be very rapid. Dolphins seen 'motionless' in the bow wave may have been using rapid tail oscillations of very small amplitude, causing them to appear to be motionless. If such swimming motions were in fact occurring, it is curious that the use of this propulsive technique should be confined to the immediate vicinity of the bow, while other dolphins a few metres away always used a large amplitude vertical tail motion with a period of about half a second (at 10 knots).

I would like to know whether other observers have seen this 'motionless' swimming, and what explanations may have been given.

ALFRED H. WOODCOCK
Woods Hole Oceanographic Institution,
Mass. Jan. 30.

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Contribution No. 419

UNUSUAL PHOSPHORUS CONCENTRATIONS IN THE FLORIDA "RED TIDE" SEA WATER

By

BOSTWICK H. KETCHUM AND JEAN KEEN

Woods Hole Oceanographic Institution[1]

Beginning in late November 1946, and continuing at sporadic intervals until July 1947, a flowering of *Gymnodinium* sp. caused discolored water off the west coast of Florida. Millions of fish were killed along the coastline and this mortality was always directly associated with the presence of *Gymnodinium* (Gunter, Smith and Williams, 1947). The phenomenon has been popularly called the "Red Tide."

Under normal conditions in the sea, phytoplankton production is limited by the supply of phosphorus and nitrogen compounds. It was thought pertinent to inquire whether the tremendous populations of *Gymnodinium* observed were able to exist with the normal nutrient supply of the sea or whether additional supplies of nutrients had become available in some way to support this flowering.

Between July 22 and 24, when an intense flowering was under way near Sarasota, Florida, various water samples were obtained by Mr. William Anderson for Dr. Paul Galtsoff, U. S. Fish and Wildlife Service. These samples were preserved with chloroform and were made available for determination of total phosphorus content. Similar samples taken one month later, during a period when there was no evidence of the plankton bloom, were also analyzed for comparison.

The total phosphorus was determined by the method described by Redfield, Smith and Ketchum (1937). The results include the organic phosphorus combined in particulate matter and plankton, the organic phosphorus in solution in the water, and inorganic phosphate-phosphorus. In different stages of the cycle of synthesis and decomposition of organic matter in the sea the proportion of phosphorus in each of these fractions will differ greatly (Ketchum, 1947). The inorganic phosphorus, which is available for assimilation by the plankton, was found by Dr. R. H. Williams[2] to be undetectable in an area NE. of Key West shortly after a heavy outbreak of the Red Tide. Apparently it was all combined in one or the other of the organic fractions.

[1] Contribution No. 419 from the Woods Hole Oceanographic Institution.

[2] Personal communication.

Reprint from SEARS FOUND. JOURN. MAR. RES.

Since our analyses include all organic and inorganic phosphorus compounds in the water, they indicate the total amount of phosphorus which had been available for synthesis into organic matter. The maximum concentration of phosphorus to be expected in the sea is about 2.0 microgram atoms per liter (Sverdrup, Johnson and Fleming, 1942).

TABLE I.—Total Phosphorus Content of Water

Samples Taken Off Florida Coast During and After the Flowering of *Gymnodinium* Sp. (Red Tide).

Location and Condition of Water in July	*July, 1947*		*August 22, 1947*	
	Salinity °/₀₀	*Total P.* *μg. at./L.*	*Salinity* °/₀₀	*Total P.* *μg. at./L.*
A. 5 mi. off Sarasota Point; 50 yards outside amber water.	32.9	2.48	33.4	0.81
In water of deep amber color.	33.2	20.4	—	—
B. 3½ mi. off Sarasota Point; water, deep amber color.	32.5	8.80	33.6	1.00
C. 1 mi. south of Sarasota Point; water, light amber color.	33.2	4.92	32.9	1.22
D. 1½ mi. off Sarasota Beach and 1½ mi. above Pt. O'Rocks; water, deep amber color.	32.5	14.6	33.2	1.08
E. 3 mi. off Musketeer's Pass; water, deep amber color.	33.2	5.96	33.6	0.62
F. 3 mi. up from Venice Inlet ½ mi. off beach, in clear blue water.	33.2	1.15	—	—

The locations of the collections are shown in Fig. 2 and the results of the analyses in Table I. In July the samples of water taken outside the discolored area contained normal phosphorus concentrations. Within the discolored area, however, the total phosphorus content varied from 4.9 to 20.4 microgram atoms per liter. This is approximately 2½ to 10 times the normal expected concentration. The samples taken in the same places in August contained between 0.62 and 1.22 microgram atoms per liter and were, consequently, all within the range to be expected in sea water. The salinity data indicate that there was little difference in the amount of fresh water present at the times of sampling. According to Parr (1935) the salinity of the offshore water in this area is about 36°/₀₀. These water samples, therefore, contained no more than 10% fresh water derived from rain and drainage.

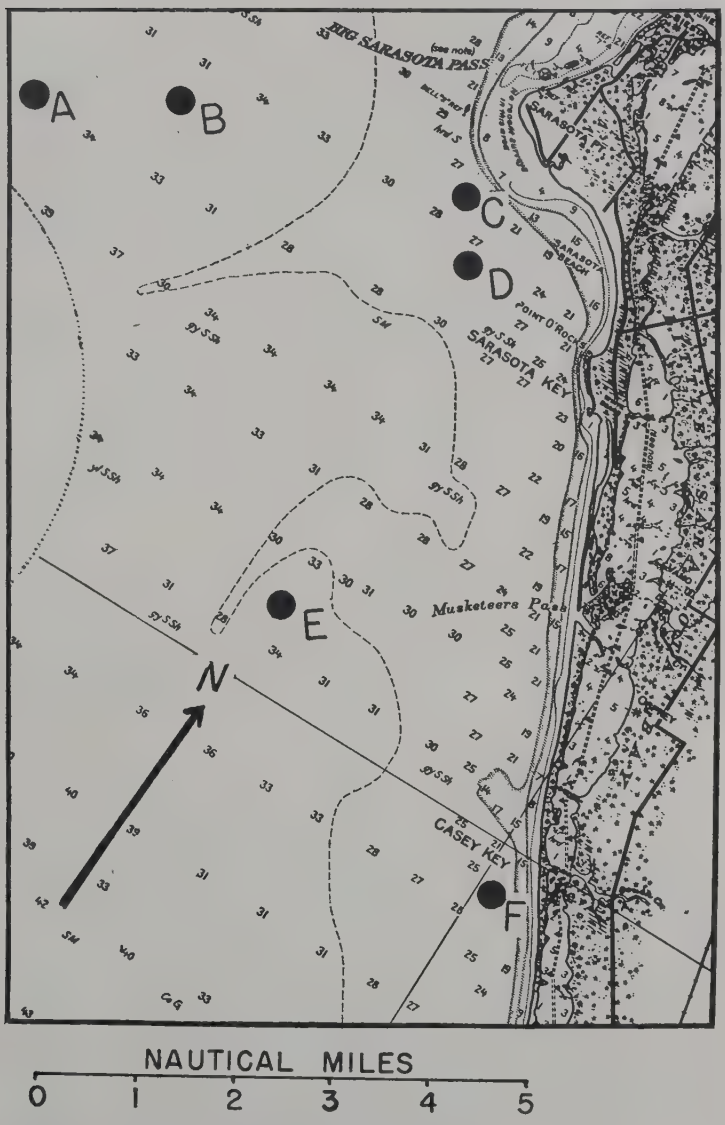

Figure 2. Section of chart off Sarasota, Florida, showing locations where water samples were taken. The depths are in feet at mean low water.

Discussion

The available data on the distribution of phosphate-phosphorus in this general area are meagre. Riley (1937, 1938) and Rakestraw and Smith (1937) found surface concentrations of 0.02–0.5 microgram atoms per liter in this general area and in the Caribbean. The latter authors found maximum values of 2.0 microgram atoms per liter at depths of 500–2000 meters. The water which supported the large populations of *Gymnodinium* thus contained more phosphorus than is present in any of the major water masses of the area. This fact excludes the possibility that the flowering can be attributed to the upwelling of nutrient-rich, deep water from the mid-Gulf.

Two processes which might explain such high concentrations of phosphorus may be postulated. The excessive nutrient content may be the result of terrigenous contamination or fertilization of the waters, or it may be the result of active swarming of the organisms.

If it is the result of terrigenous contamination, an enormous quantity of phosphorus must be contributed to account for the extent of the flowering. The water in this area is on the average 10 meters deep. If the phosphorus is uniformly distributed to this depth, an average total of 3–6 grams per square meter of sea surface would be present. The addition of 3 grams of phosphorus per square meter would require about 17,000 pounds of pure phosphorus per square mile (*i. e.*, about 340,000 pounds of "Superphosphate" fertilizer containing 5% P). The reports of the extent of the flowering indicate that areas of several square miles were affected. The salinity data show that there was little or no excess fresh water drainage in the July samples, and it seems unlikely that the drainage water would vary so tremendously in its phosphorus content. Therefore, the possibility that water-borne contamination has caused these results seems unlikely.

It is conceivable that the *Gymnodinium* could assimilate all of the phosphorus of the water column and subsequently swarm at the surface, thus giving rise to the observed high concentrations. Using again the average depth of 10 meters, if all of the phosphorus were concentrated in a surface layer one meter deep, a tenfold increase would thus be accounted for. The *Gymnodinium* cells have been observed to accumulate at the surface of jars of sea water collected from the affected area. Such accumulation in the open sea, however, would require very calm conditions so that the mixing of the water and the resultant downward transport of the cells would be at a minimum.

To differentiate between these two possibilities, water samples from various depths in the affected areas should be analyzed. External contamination would be indicated if the total phosphorus content of the water column were greater than would be expected from the

normal content of the sea. The distribution and source of this contamination could be traced easily by the proper spacing of sampling locations. Determination of the carbon : nitrogen : phosphorus ratios of the plankton cells would show whether phosphorus alone or a "balanced fertilizer" had been the contaminant. On the other hand, if most or all of the phosphorus of the water column were concentrated in the surface layers, swarming of the *Gymnodinium* cells would be suspected. This note is presented in the hope that future investigation of similar phenomena will give an answer to this problem.

Summary

1. The total phosphorus content of waters containing dense *Gymnodinium* populations was found to be 2½ to 10 times the maximum to be expected in the sea. The possibility that upwelling of nutrient-rich, deep water is the explanation of this intense plankton bloom is thereby excluded.

2. It is suggested that future studies of intense plankton blooms include total phosphorus determinations at various depths. The results would differentiate between terrigenous contamination and swarming of the organisms at the sea surface.

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Contribution No. 420

Transactions, American Geophysical Union Volume 29, Number 6 December 1948

OCEAN CIRCULATION IN MARSHALL ISLANDS AREA

C. A. Barnes, D. F. Bumpus, and John Lyman

(Contribution No. 420, Woods Hole Oceanographic Institution)

Abstract--Salinity and temperature observations were made from Naval vessels during Operation Crossroads for the purpose of determining the probable drift of radioactive material around Bikini. These observations have been subjected to water-mass analysis, and dynamic computations have been carried out. Results are compared with Japanese and other data from the region. Approximate temperature-salinity correlations at different latitudes in the transition from the deeper Pacific Equatorial Water to shallower western North Pacific Central Water are shown.

Introduction--As a part of Operation Crossroads, an oceanographic survey was conducted to provide information on the probable drift of radiologically contaminated water away from Bikini Atoll. This survey was made during the months of March to August 1946. A total of 240 temperature-salinity stations was occupied in the Marshall Islands area between the parallels of 3°S and 20°N and the meridians of 162°E and 172°E. Although the larger number of these stations was within a 100-mile radius of Bikini, four sections were extended south across the Equator and two north to latitude 20°N. The coverage is most representative of the summer months of July and August. At the time the expedition was organized the only available deep-water observations were those from three stations in the northern part of the area occupied by the Carnegie in May 1929 [FLEMING, ENNIS, SVERDRUP, SEATON, and HENDRIX, 1945, pp. 226-227]. Figure 1 shows the location of the Carnegie and Crossroads stations. Data from approximately 400 Japanese stations occupied in this general area during the period 1935 to 1942 have since become available. These data have been superficially examined and compared with the Crossroads observations, but time has not permitted a detailed analysis.

Crossroads observations were made with common oceanographic techniques, using Nansen bottles and protected and unprotected reversing thermometers. Lowerings of 900-ft bathythermographs were also made at each station to supplement temperatures obtained from the reversing thermometers. The observations were made from five naval vessels, four being used simultaneously during late June and July, and two early in August.

Because of the recent War, many of the thermometers used lacked calibration certificates and those having certificates had not been checked for many years. The thermometers are now being calibrated. Preliminary determinations indicate an average change in the ice point of 33 thermometers of +0.03°C, with a range from 0.00 to + 0.06°. Although it is not expected that the general picture of circulation in the area will change when corrected values are available, detailed topography of particular localities may vary, and the depth and temperature observations reported herein are to be regarded as provisional. Unfortunately, not all the salinity samples were titrated, and for the purposes of this discussion the missing salinities have been estimated from temperatures using the temperature-salinity correlation for the appropriate latitude.

General--The predominating currents in the vicinity of the Marshall Islands are the westerly-directed North Equatorial Current north of latitude 6° or 8°N and occupying the area of the northeast trade winds, the easterly-directed Equatorial Counter Current in the doldrum belt between the North Equatorial Current and the vicinity of the Equator, and the South Equatorial Current setting west, south of the Equator. Boundaries of these currents are considered as shifting northward with the Sun in northern summer and southward in the winter. Water masses of primary interest in this region are the western North Pacific Central Water occupying the area north of the Equatorial Counter Current, and the Pacific Equatorial Water in the area of the Counter Current (see Fig. 2). On the south, the area borders on western South Pacific Central Water. A subsurface intrusion of Intermediate Water from the zone of Subarctic Convergence may be found in the northern part of the area.

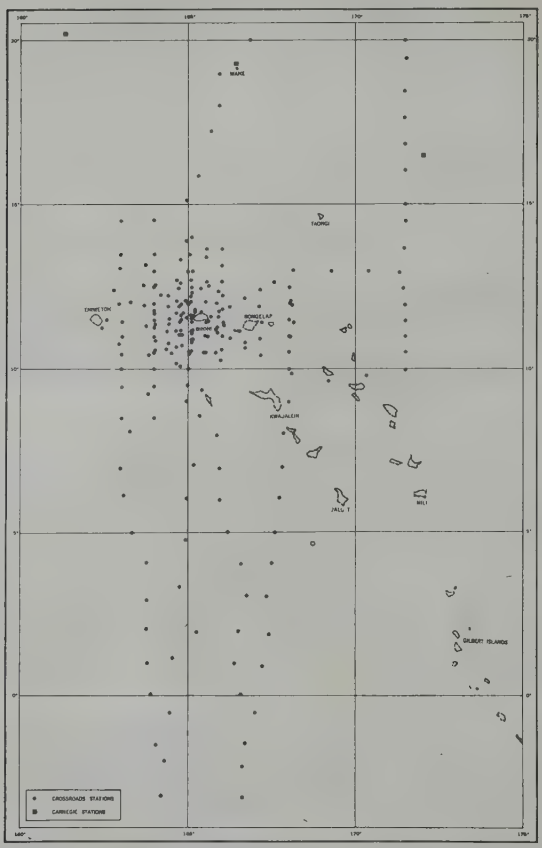

Fig. 1--Positions of Carnegie (1929) and Crossroads (1946) oceanographic stations

Temperature--In general, the vertical temperature distribution consists of a virtually isothermal layer from the surface to 75 m, a strong main thermocline from 150 to 300 m, and a deep, weak gradient below 300 m toward the bottom. The temperature ranges from 27° to 29°C at the surface (temperatures slightly less than 26°C at the surface have been reported for the northern part of the area during earlier months of the year) to about 10°C at 300 m and to about 3°C at 1500 m.

The north-south distribution of temperature is illustrated in Figure 3, a profile of temperature along the meridian of 166° E (longitude of Bikini). The shallower isotherms, which are nearer the surface in the center of the area, latitude 7°N, corresponding to a region of low salinity, dip toward the north in the region of the Northern Equatorial Current and then rise from latitude 17°N in what appears to be transport in an easterly direction. This inclination of the isotherms is also apparent in the Japanese data collected in the region.

Commencing at latitude 7°N, the shallow isotherms dip slightly toward the south, the maximum slope occuring in the region of the Equatorial Counter Current. The sharp dip in the 10°C isotherm is evidence of the intrusion of western South Pacific Water.

Salinity--The salinity distribution is depicted by Figure 4, a profile of the same stations as shown in Figure 3. The center of the area between 3°N and 11°N is occupied by water of relatively

low salinity; there is but slight vertical structure between 7°N and 11°N. These are latitudes of high precipitation, and in addition, water of low salinity is being brought in from the west by the Equatorial Counter Current. To the northward, the surface salinities rise in the region of higher evaporation. There is evidence as far south as 11°N of the intrusion of North Pacific Central Water under the less saline surface water. This is borne out by the appearance of the 35 0/00 isohaline.

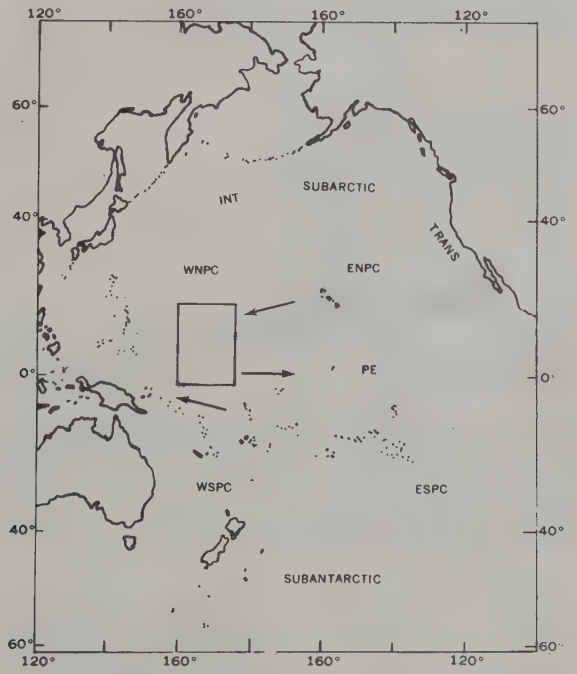

Fig. 2--Pacific Ocean showing water masses [after SVERDRUP, JOHNSON, and FLEMING, 1942] and region in which Crossroads oceanographic stations were occupied; arrows show the set of currents; abbreviations; INT, Intermediate Water; TRANS, Transition Region; WNPC, western North Pacific Central; ENPC, eastern North Pacific Central; PE, Pacific Equatorial; WSPC, western South Pacific Central; PE, Pacific Equatorial; WSPC; western South Pacific Central; ESPC, eastern South Pacific Central

An intrusion of western South Pacific Central Water with relatively high salinity crosses the Equator from the south under the less saline Equatorial Counter Current, as shown by the 34.8 0/00 isohaline and the 10°C isotherm. The region between latitudes 4°N and 11°N appears at shallow depths to be that of vertical mixing of the fresher surface water as described by SVERDRUP, JOHNSON, and FLEMING, 1942, p. 711] and of lateral mixing at greater depths of the more saline waters from the north and south. The sigma-t surface of 26.0 is shown extending from water of 35.4 0/00 on the south to 34.4 0/00 water on the north. The underlying water is Pacific Equatorial Water, which is present near the surface (300 m) to latitude 12°N and deepens to 1100 m at 20°N. Between the Pacific Equatorial Water at depth and the western North Pacific Central Water near the surface, there is an intrusion of Intermediate Water of the North Pacific. This is shown by the 34.2 0/00 isohaline at 600 to 700 m.

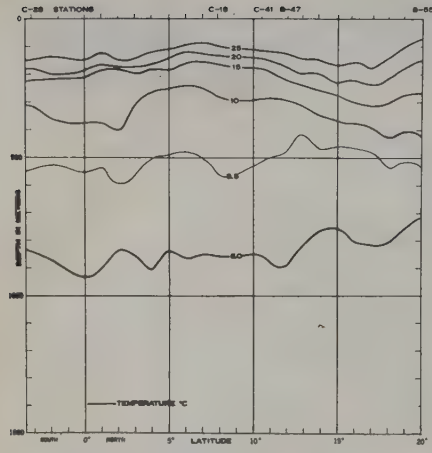

Fig. 3--Vertical temperature distribution along the meridian of Bikini (166°E)

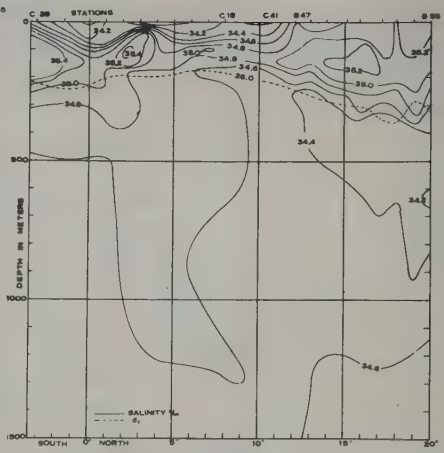

Fig. 4--Vertical salinity distribution along the meridian of Bikini (166°E)

Figure 5 shows the temperature-salinity relationships of the western North Pacific Central Water and the Pacific Equatorial Water as defined by SVERDRUP, JOHNSON, and FLEMING, 1942, pp. 706-745]. The solid lines in the left side of the diagram show approximately the appearance of the temperature-salinity correlations at different latitudes in the transition from the deeper Pacific Equatorial Water to the shallower western North Pacific Water. At latitude 20°N the water is all North Pacific Water; at 15°N the transition zone commences at 700 m (see the insert to Fig. 5) and ends at 400 m; while at 10°N the transition zone lies above 200 m and is less than 50 m thick.

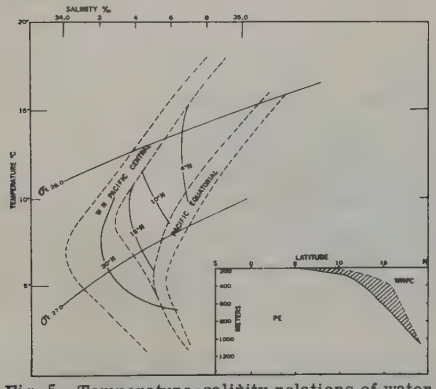

Fig. 5--Temperature-salinity relations of water masses in Marshall Islands area

Dynamic topography--The dynamic topography of the area has been computed from the temperature-salinity-depth measurements. Figure 6 shows anomalies of dynamic heights of the surface expressed in units of dynamic centimeters and referred to the 1000-decibar level. The contours indicate a generally westward set of the current between the latitudes of 8°N and 17°N. The drift of this North Equatorial Current averages approximately one-third knot over most of this latitude range, but is variable with a maximum of nine-tenths knot west of Bikini Atoll. The presence of eddies northwest and northeast of Bikini is indicated. Japanese data also show a probable eddy to the northeast, but stations were too widely spaced to confirm the leeward eddy. Drift-pole studies conducted in April and May showed a westerly set south of Bikini Atoll with drift rates varying from 0.3 to 0.4 knot at a distance of ten mi south of the periphery of the atoll to one knot within a distance of two mi of the islands. Although the general drift of the poles was westerly, they drifted northwest south of the eastern end of the atoll, changed to west as they approached the atoll, and shifted southwest near the western end of the atoll. This drift roughly parallels the 190 dynamic cm contour shown for that vicinity in Figure 6 and indicates that the detailed topography may be quite complex. The two island chains terminating near the latitude of Bikini no doubt contribute to the complexity of the local surface topography of the area. The apparent reversal of current between latitudes 6° N and 9° N may be a partial result of the damming of the flow by the closely grouped atolls to the east.

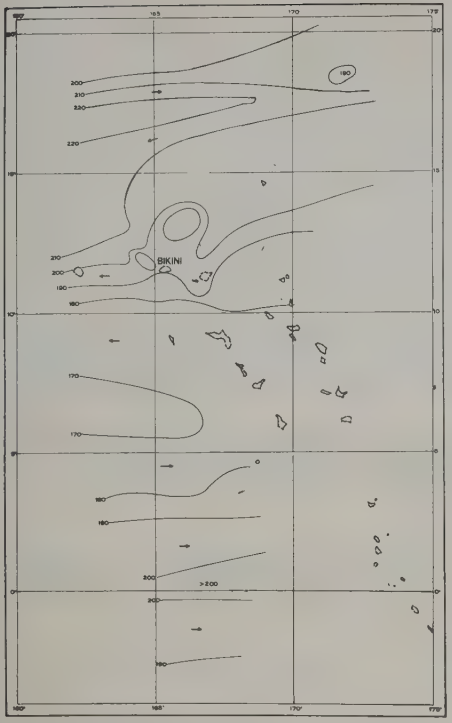

Fig. 6--Dynamic topography of the sea surface relative to the 1000-decibar surface, Marshall Islands area, in units of dynamic centimeters

North of 17°N the contours show an easterly setting current of approximately 0.8 knot, but measurements at this latitude are too few to exclude the possibility of an eddy. South of 7°N the Equatorial Counter Current sets eastward. The velocities obtained from dynamic calculations were as high as two knots, but the use of the Bjerknes method at these low latitudes is open to question.

Related temperature measurements were made and salinity samples taken over a 20-hr period at one location near Bikini (lat. 11°28′N, long. 165°15′E). The anomalies of dynamic heights of the surface referred to the 300 decibar level for nine series of measurements varied from 118 to 123 dynamic cm, with an average deviation of 1.3 dynamic cm and a probable variation of each determination from the mean of 1.6 dynamic cm. It is believed that this variation is largely occasioned by internal waves. Using these observed values as a basis and assuming a station spacing of one degree of latitude (60 mi), variations at one station alone would cause computed currents to fluctuate by the amounts shown in Table 1 at different latitudes.

If one station were occupied at the crest of the wave and the other at the trough the fluctuations would be double the above values. The existence of internal waves is confirmed by bathythermograph studies which are the subject of the paper by LA FOND [publication pending].

The same general pattern of dynamic topography prevails at 300 m as at the surface, but calculated velocities are less than one-third those at the upper level. Figure 7 shows smoothed

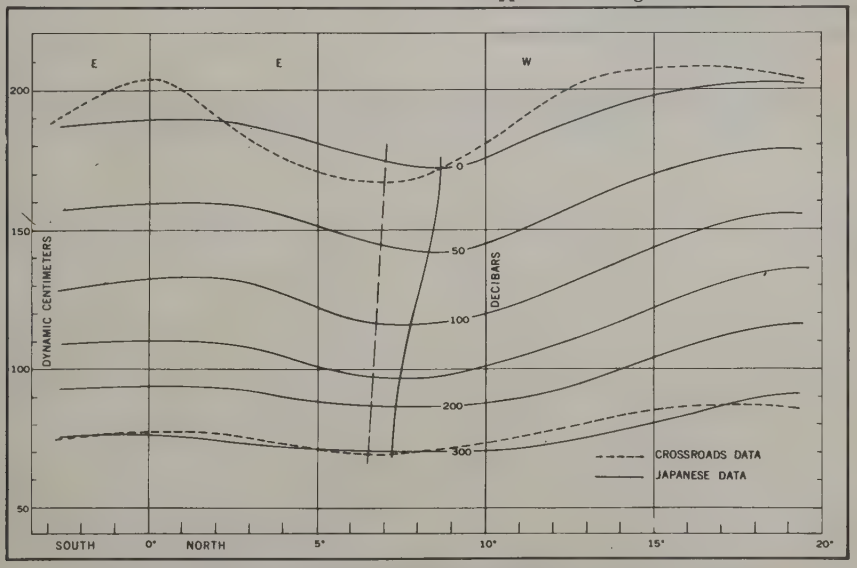

Fig. 7--Smoothed profile of isobaric surfaces relative to the 1000-decibar surface, Marshall Islands area

profile isobaric surfaces for north-south sections as obtained from the Crossroads (broken line) and Japanese (solid line) data. The averaging of dynamic heights for increments of latitude for this area obscures details of topography and effects of internal waves but stresses the persistent features. Both sets of observations show the boundary between the east- and west-setting currents at approximately latitude 7° or 8°N, the pronounced current toward the west between 8° and 15°N, and a slackening or reversal north of about 15° to 17°N. Crossroads data show the Counter Current extending south past the Equator, whereas the Japanese data indicate no definite direction south of about 2° or 3°N. Currents south of 10° are confined almost entirely to the upper 300 m.

Table 1--Fluctuation of the current

Latitude	Fluctuation in calculated current
°	knot
2	0.5
3	0.4
4	0.3
5-7	0.2
8-20	0.1

The profile of the sea surface based on Crossroads data shows a pronounced maximum at the Equator, in agreement with theory which requires of isobaric surfaces maxima or minima at that latitude. The other surfaces depicted in the vicinity of the Equator are quite flat, with maxima or minima too poorly defined to be of much significance in support or contradiction of theory.

Acknowledgments--The authors are deeply indebted to the Naval personnel of the participating vessels and to the many civilian observers whose cooperation and efforts have contributed so much to the collection and analysis of the information upon which this paper is based.

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(Manuscript received May 13, 1948; presented at the Twenty-Eighth Annual Meeting, Washington, D. C., April 28, 1947; open for formal discussion until May 1, 1949.)

Contribution No. 421

THE CIRCULATION SYSTEMS OF BIKINI AND RONGELAP LAGOONS

William S. von Arx

(Contribution No. 421 of the Woods Hole Oceanographic Institution)

Abstract--Four and one-half months of the early part of 1946 were spent in the field at Bikini and Rongelap Atolls to study the circulation systems within the lagoons. Additional synoptic studies were made in the laboratory of kinematically similar models based on early field data. The results of these studies were later tested against further observations made in the field. It was found that both lagoons exhibited a primary circulation (overturning wind-driven circulation) and a secondary circulation (rotary circulation composed of two counter-rotating compartments). The direction of the primary circulation and the division between the counter-rotating compartments of the secondary circulation were always contained in a vertical plane having roughly the azimuth of the prevailing wind. The vigor of both circulations varied with the average wind strength taken over the previous 24 hours. Perturbations of the primary and secondary modes of circulation were produced by tides, waves, and the North Equatorial Current which surrounds the atolls of the northern Marshall Islands group. Seasonal changes were also noted; the circulation of the winter months when the northeast trade-winds prevail showed a marked stability and strength which was lacking in the summer season when the atolls are on the edge of the belt of doldrums.

In addition to the qualitative synopsis of the circulations, numerical data are presented in tabular form which show the volumetric exchanges of water between the lagoons and the ocean. An estimate is made of the rates of refreshment and overturning of each lagoon. A chart of the values of eddy diffusion in the surface plane is given for Bikini, as well as secondary data on the behavior of current poles and dye trails in a variety of wind and current strengths.

Introduction--The greater part of the field data for this study was accumulated at Bikini Atoll in the course of four and one-half months residence there. The data from Rongelap Atoll were gathered in the course of only six days. The data are probably more representative than the period of observation suggests, for the work at Rongelap was executed by a relatively large force and planned in the light of the experience gained and techniques used at Bikini. Nevertheless it should be assumed that all generalizations and discussions of principle are based upon observations made at Bikini and apply only to Bikini unless specifically extended to include Rongelap.

Inspection of Table 1 will show that the dimensions of Bikini and Rongelap Lagoons are so large that some means of synthesis is required to relate observations made at separated points.

Table 1--Comparative physical dimensions of Bikini and Rongelap

Specification	Bikini	Rongelap
Approximate volume	5.0 mi^3	8.5 mi^3
Approximate area [NUGENT, 1946, p. 748]	192 mi^2	305 mi^2
Total reef length [NUGENT, 1946, p. 748]	57 mi	80 mi
Length of reef awash	29 mi	53 mi
Length of island strip	13 mi	18 mi
Width of passes and channels	15 mi	9 mi
Average depth of lagoon [NUGENT, 1946, p. 748]	26 fm	28 fm
Average depth over reefs awash	1/2 fm	1/2 fm

Therefore, in addition to field work, two months were spent in the laboratory to develop a technique whereby the observations made in the field could be reproduced in kinematically similar models and the circulations studied synoptically. Two models were built of Bikini on a scale of 1/100,000 and one of Rongelap on a scale of 1/150,000. These were placed separately in a flow tank and subjected to appropriately scaled ocean current, wind, waves, and tide. The behavior of each model was adjusted to resemble its prototype at all the points observed in the field and the resemblance was assumed to hold for all points in between. A total of over 60 points representing more than 100 stations and repeated stations was available for the Bikini models, and 37 single observations were available for the Rongelap model. It is through study of these models and the field data that the selection was made of the most probable circulation hypotheses.

Discussion of results--Four sources of energy have been found to drive the circulation within Bikini and Rongelap Lagoons: Wind, waves, tides, and the North Equatorial Current. Most of the water motion of the lagoons is produced by wind traction on their surfaces. The exchange of lagoon water with that of the sea is accomplished in winter (the trade-wind season) by tides and wave action, and in summer (the doldrum season) by tides and the North Equatorial Current. The change of agencies occurs with the seasonal migration of the northeast trade-wind belt which moves northward in summer, leaving the northern Marshall Islands more or less becalmed in the doldrums. The effect of the presence or absence of the trade-winds is so marked that constant reference to them must be made in order to present the field data and circulation hypotheses intelligibly.

The effect of the active forces is determined as much by the solid physical structures of the atolls as by the forces themselves. Each lagoon is essentially a "lake in mid-ocean," cupped in a shallow saucer-like basin supported by a solitary mountain peak. From a remote vantage point southeast of the atolls they must appear somewhat as shown in Figure 1. The atoll structures rise abruptly from the ocean floor, which in this region lies at a depth of about 2000 fathoms. Between the atolls, and sometimes coalescent with them, there are flat topped seamounts, which HESS [1946] has described and called "guyots." These fail to reach the surface by six or seven hundred fathoms. Both the guyots and atolls obstruct the flow of the North Equatorial Current and

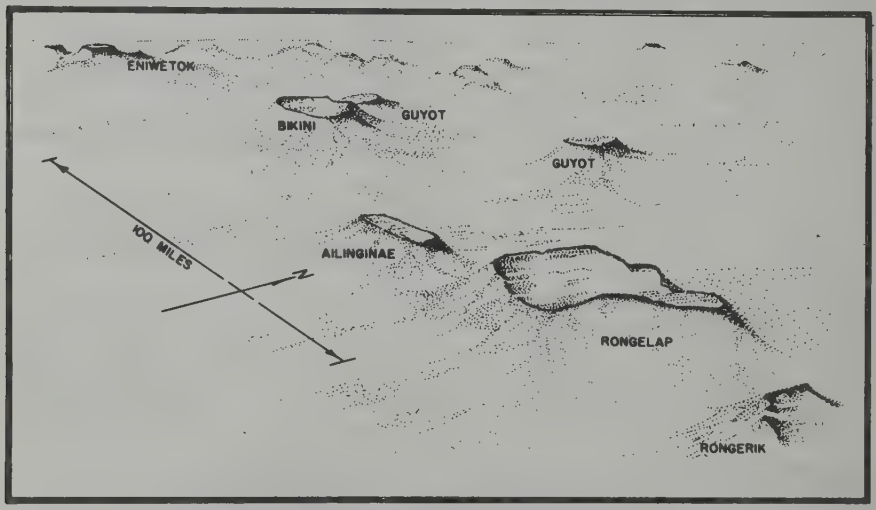

Fig. 1--Rongelap, Bikini, and their surroundings, as they would appear from the southeast with the water removed

confuse its westward motion through the area. Waves and swell also progress westward through the atolls during the trade-wind season and pound systematically on the eastern and northern reefs. As a result of this pounding and the asymmetrical supply of nutrient materials from the sea, the windward reefs are concave upward while the leeward reefs are convex upward.

Along most of the length of the concave windward reefs there is a broad water-filled terrace fenced in by the island strip on the lagoon side and a cavernous bulwark of coral and algae on the seaward side, shown in section in Figure 2. The cavernous structure is honeycombed with rooms connected to the sea by surge channels. Cracks in the arches of the rooms are open to the sky. Swell rammed up the surge channels fills the rooms and forces water upward through the cracks and onto the terrace. The surface of the water on the terrace was measured repeatedly by H. J. Turner at a level 0.5 m higher than the level prevailing in the lagoon. In response to this steady head the terrace water flows between the islands into the lagoon. At Bikini several hundred photographic measurements made with dye bombs dropped on the reef from aircraft show an average inward velocity of flow of nearly 50 cm/sec. The flow is continuous throughout the trade-wind season and supplies approximately one-third of the volume of new water added to the lagoon each day. During the doldrum season, when the ocean swell is much reduced, the inflow becomes negligible or even reversed.

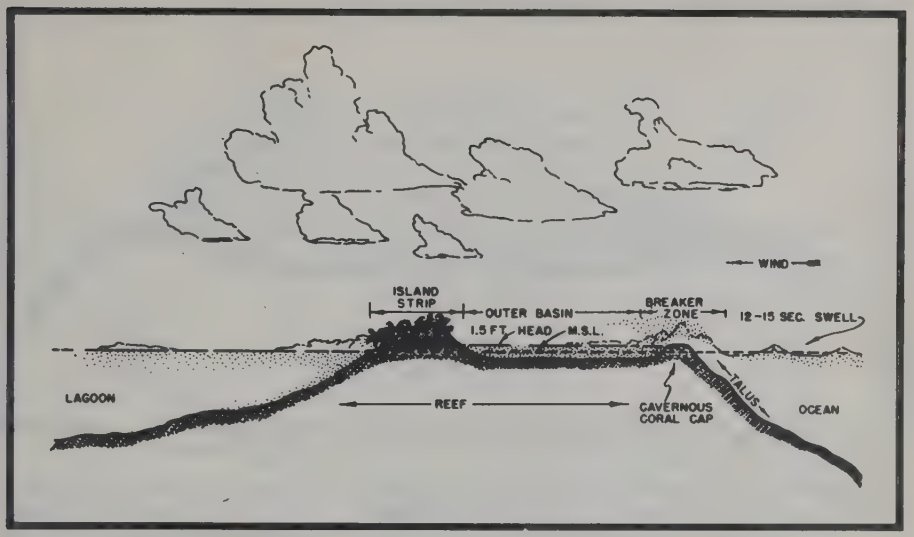

Fig. 2--Mechanism of constant inflow across windward island strip

Over the rounded leeward reefs similar aerial observations of the flow show that the water transport alternates with the tides. The leeward reefs are submerged so that waves cross them, but since leeward waves are those which have been diffracted around the whole atoll, their energy is small and their approach oblique. The water driven by the wind along the surface of the lagoon toward the leeward reefs causes the flow over them to be predominantly seaward. During the doldrum season when the wind-driven surface current moves more slowly the tidal alternations of flow are more symmetrical.

The stress of the wind on the lagoon surfaces moves a layer of water along with it. Well over 100 current measurements at 34 stations at Bikini show the thickness of the surface layer to change with the strength of the wind from five to 20 m and its speed to be very close to three per cent of the average wind speed taken over the previous 12 hr. The thickness of the surface layer in winter is usually 13 m and its average speed is 25 cm/sec. In summer these values drop to an average thickness of nine m and a speed of less than 15 cm/sec.

Throughout both the summer and winter seasons in both lagoons the volume of water transported in the surface current is too great to be exhausted through the leeward passes or over the leeward reefs; consequently some of the water sinks and returns upwind along the bottom as shown in Figure 3. The bottom current is much thicker and slower than the surface current. It links the two ends of the surface current and produces a closed circulation which constitutes the primary overturning circulation system found in both lagoons.

The volume of water transported by the bottom current is somewhat greater than that carried by the surface current. When the bottom current reaches the lee of the windward reefs the water is forced upward. The greater portion finds its way back into the surface current, but a small fraction of the upwelling water diverges in the lee of Bikini Island at Bikini and in the lee of Eniaetok Island at Rongelap and flows in opposite directions along the reef. Measurements made at Bikini show the wind-driven surface layer to be less than two m thick within 3000 m of the lee of islands along the windward reef, and within 2200 m in the lee of open reef. The fetch needed to produce a wind-driven surface current of normal thickness has been arbitrarily chosen as the width of the zone of upwelling. The divergent currents within this zone and their extensions along the reef constitute the secondary circulation system found to exist in both lagoons.

The secondary circulation, shown in Figures 4 and 5, divides the lagoons into two counter-rotating compartments which move in a clockwise sense in the southern portions and in a counter-clockwise sense in the northern portions. Beginning at the line of divergence in the lee of the windward reefs, a longshore current occupying the full depth of the lagoon basin can be traced in either direction. Both currents travel about half the lengths of the lagoons along the northern

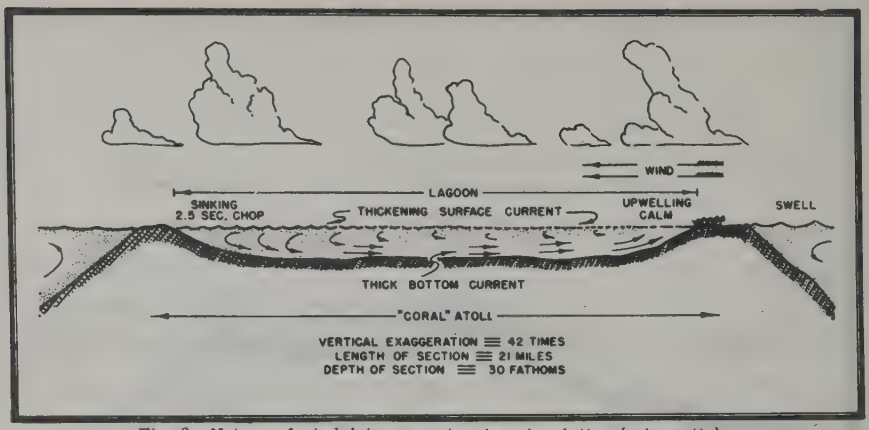

Fig. 3--Nature of wind driven overturning circulation (schematic)

and southern reefs respectively. In each case the longshore current is confronted by a salient in the reef which turns the current into the body of the lagoon. At each of these points the current sinks and becomes part of the bottom current where it is indistinguishable from the primary circulation system.

At Bikini, where this mechanism was discovered, the southern branch of the longshore current crosses the mouth of Enyu Channel. The channel is only 14 m deep so that the bottom current has little chance of access through it to the sea. A current of ocean water sweeps around Enyu Island and enters the lagoon through the eastern third of Enyu Channel at a speed of from 20 to 40 cm/sec. The southbound longshore current heading for the same part of the channel at a speed of 15 cm/sec.is forced upward and westward by the bend of the reef in the lee of Enyu Island and then encounters the incoming ocean water. The result of this encounter is the Enyu spiral, a slowly spiralling stream of water moving westward along the southern reef and islands with a speed of from 20 to 35 cm/sec. The Enyu spiral extends from top to bottom of the lagoon and is about 3000 m wide. In crossing the mouth of Enyu Channel the upper layers are bowed in and out with the changing tide. Part of the stream is split against Arji Island, at the west end of Enyu Channel with a small component escapes into the sea at a rate of 35 to 45 cm/sec. The remainder skirts the intermediate islands, and again encounters the reef at the sill of Rukoji Channel. Here the upper ten m of the stream goes out to sea, and the bottom portion is turned northward by the Rukoji sill, and eventually eastward by the primary circulation, to become part of the normal bottom current. The bottom current is gathered from the western third of the lagoon, but it is not until it is augmented by the remains of the Enyu spiral and its counterpart along the northern reefs, which joins the flow at a point half way between Yuro and Namu Islands, that it assumes its full strength. The interaction of ocean water with lagoon water in the Enyu spiral generally produces water of lower salinity than is found elsewhere in the lagoon.

In summer the Enyu spiral probably ceases to exist, for under the influence of light southeasterly summer winds Enyu Channel becomes a strong source of incoming ocean water. This forces a reorganization of the secondary circulation system.

The flow through the southwest passes and channels is predominantly tidal. Despite the fact that these gaps in the reef are direct openings to the sea in which tidal currents move at speeds sometimes approaching 150 cm/sec, they produce only a small effect upon the lagoon circulation and its refreshment rate. This is due to the fact that the water entering the lagoon on the flood tide through a pass does not get far from the mouth of the pass before the tide changes and draws most of it out again. It is estimated that only 30 per cent of the water entering a pass on the flood tide remains in the lagoon at the completion of the ebb tide. This remainder is the quantity which was moved away from the influence of the pass by the primary lagoon circulation. On the flood tide, currents radiating from the southwestern passes were detected 5000 m inside the lagoon, but not all the water moving in response to the flow in the passes comes through them; hence the radius of direct refreshment around the passes is probably somewhat less than 5000 m.

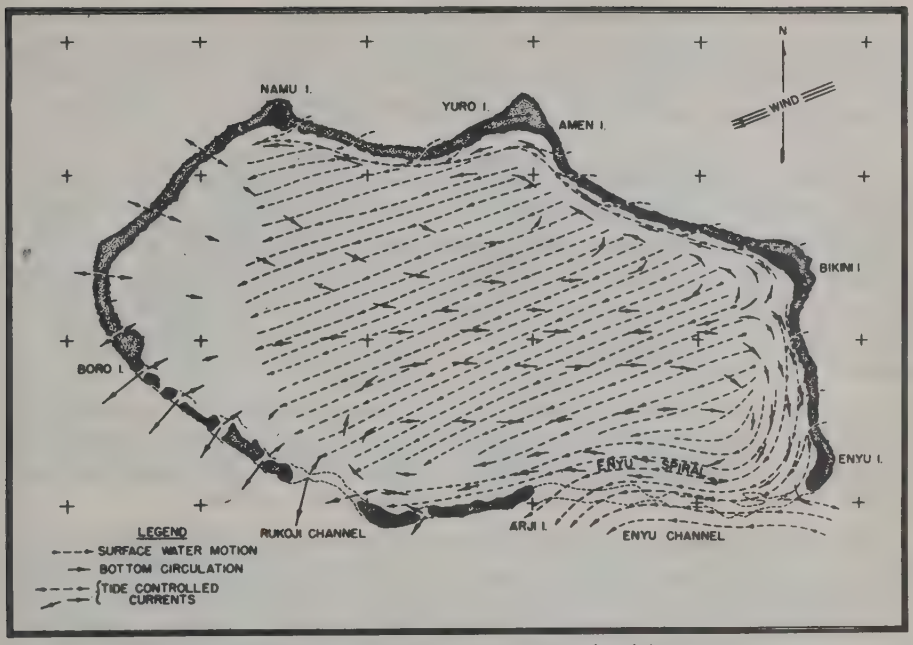

Fig. 4--Generalized circulation of Bikini Lagoon in winter

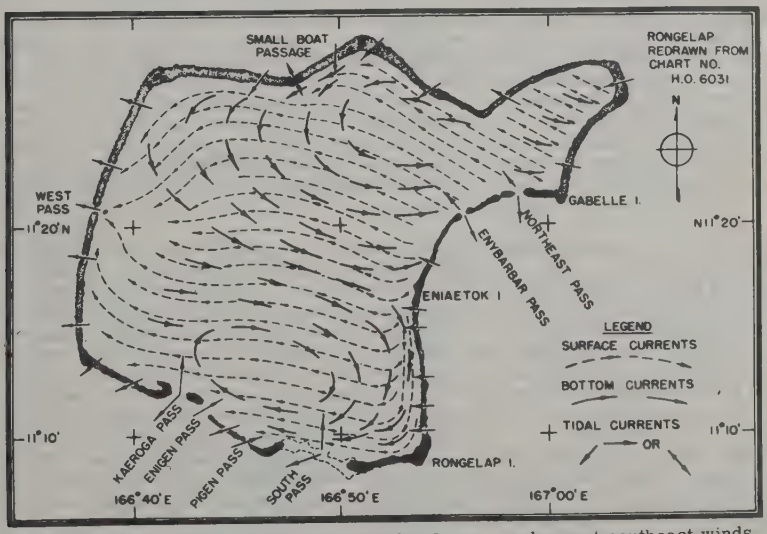

Fig. 5--Generalized circulation of Rongelap Lagoon under east southeast winds

The southwestern passes at Bikini were studied intensively both from the air and from shipboard. It was found that the flow through them was 40 per cent stronger on the ebb tide than on the flood. This condition counteracts in part the continuous inflow of water over the windward reefs in winter and the inflow through Enyu Channel in summer. The current through the passes is hydraulically induced by the difference in level between the ocean and the lagoon. The ocean

rises and falls as a simple harmonic oscillator, but the lagoon level, restricted by the limited capacity of the passes to transport the required volumes and the constant inflow of water over the windward reefs, cannot keep in step. The lagoon surface probably oscillates through a slightly smaller amplitude than the ocean surface and is somewhat out of phase in the vicinity of the passes. The turn of the current in the passes is 25 min later than high water in the ocean and ten min later than low water in the ocean. The duration of slack water is less than two min.

This situation is even more marked at Rongelap because the proportion of lagoon volume to cross-sectional pass area is 3.5 times greater. This results in a larger head of water between the inside and outside of the lagoon during the mid-stage flood and ebb tides, which causes the water to flow much farther into the lagoon and take the form of a jet. Observations of the flow through three of the passes and simultaneous measurements as much as 8000 m inside the lagoon along the jet detected the arrival of the flooding current. Model studies of the same phenomenon indicated the length of the incoming column of the largest jet from Kaeroga Pass to be 10,000 m and water to be pushed ahead of the jet as far as 12,000 m from the pass. It is expected that the Kaeroga jet returns to the sea on the ebb tide considerably less water than would retrace its course through a corresponding pass at Bikini. The South Pass jet is probably more nearly comparable to Bikini passes.

West Pass in the middle of the leeward reef at Rongelap (see Fig. 5) is unusual in that it is constantly outflowing. It is probably one of the principal exits for surface water driven by the wind toward the western side of the lagoon. Current poles as much as 5000 m on either side of this pass were drawn toward it and eventually passed through it. The current speed in the pass has been conservatively estimated at between 250 and 500 cm/sec.

The exchange budgets--The following tables summarize the quantitative results of the circulation studies, and are based entirely upon field observations. Despite the abundance of data for the water motions in the lagoon derived from current meter stations, current pole runs, dye drift experiments and bombing runs, and secondary evidence of geological and biological sorts, there are a number of important parameters which have been evaluated by means of an educated guess. These parameters are chiefly those needed to convert velocity data into transport data and involve estimates of the average depth of water over different reef sections, correction for the sinusoidal rate of flow of tidal currents, a correction for the observed maximum current to average current through the passes [SVERDRUP and others, 1942, p. 568], and an assumed steady state during the winter months. These assumptions are evaluated as follows: Average depth of water over the reefs (winter), 100 cm; correction for flow in passes, $V_{aver} = 0.75\ V_{max}$; and correction for sinusoidal tidal flow, $2/\pi$. A further distinction in tabulating the data is made for channels and passes. Channels are broad shallow openings in the reef for which V_{max} and V_{aver} are substantially the same. Passes are narrow V-shaped openings in which bottom and side fraction have important effects upon the measured maximum and average rates of flow. For this reason distinctions are made between passes and channels, and where composite features exist as in the case of Rukoji Channel which has a pass-like notch in its sill, the flows through the pass and channel portions have been separated.

Tables 2, 3, and 4 present data used in computing the volume of water involved in a tidal cycle during the trade-wind season, and show that the volume is approximately 1,060,000 m^3. The total volume of Bikini lagoon is approximately 28,000,000 m^3. Thus 3.8 per cent of the lagoon's volume is transported into and out of the lagoon per tidal cycle. Using this rate it requires about 13 days for the lagoon to exchange its own volume with the sea. This procedure tacitly assumes that every particle of incoming water is retained in the lagoon and every particle of exhausted water is lagoon water. This is inexact to the extent that the passes exhaust on the ebb tide about 70 per cent of the ocean water introduced on the previous flood. Thus the rate of exchange is reduced by an amount which is proportional to the ratio between the rate of exchange through the passes and the "rectified flow" over the reefs. This yields a correction factor of about 3.0, making a more reliable estimated rate of exchange with the open ocean one lagoon volume in 39 days. This value is valid only during the trade-wind season when a steady state can be assumed. Throughout the summer season no prolonged steady state exists, but it was found that the flow through the passes is reduced 50 per cent and that over the reefs nearly 80 per cent. The change in average wind direction from easterly to southerly occasionally forces water out of the lagoon over the northern reefs and makes Enyu Channel an important source of incoming water. It is estimated that the summer average exchange rate is approximately half of the winter rate.

The rate of overturning of the lagoon's primary circulation is calculated to be once in 150 hr for the winter season and once in approximately 300 hr for the summer season.

Table 2--Calculated flow into and out of Bikini Lagoon in the trade-wind season

Reefs	Length	Depth	Velocity				Volume			
			Tide stage				Tide stage			
			High	Ebb	Low	Flood	High	Ebb	Low	Flood
	km	m	cm/sec	cm/sec	cm/sec	cm/sec	m^3/sec	m^3/sec	m^3/sec	m^3/sec
Boby-Namu	0.5	Varies	20	10	10	25	130	40	20	100
Namu-Yuro	8.4	with	40	40	30	45	4350	2700	750	3020
Amen-Bikini	9.8	stage	40	50	25	40	5100	3900	740	3140
Bikini-Enyu	5.4	of	00	40	20	30	2100	1730	320	1300
Boby-West	8.5	tide	- 0	- 15	0	20	0	- 1020	0	1360
West-Boro	6.3		- 5	- 5	5	5	- 410	- 250	90	250
						Sums	11,270	7100	1920	9170
Channels										
Rukoji[a]	3.5	8.7	- 5	- 15	- 5	45	- 1500	- 4500	- 1500	13,700
Enyu	15.7	12.2	-2.5	- 3.0	- 2.5	- 2.0	- 4800	- 5800	- 4800	- 3800
						Sums	- 6300	-10,300	- 6300	- 9900
Passes										
All SW	2.0	29.4	-10	-100	-15	50	- 5900	-59,000	- 8900	29,400
Rukoji[a]	0.6	36.6	- 5	- 25	- 5	50	- 1100	- 5500	- 1100	11,000
Eniirikku	0.4	55.0	- 5	- 25	- 5	35	- 1100	- 5500	- 1100	7700
						Sums	- 8100	-70,000	11,100	48,100
						Corrected sums for passes	- 6100	-33,400	- 8300	22,900

Positive values denote inflow; negative values, outflow.
[a]Rukoji, a "composite channel," is subdivided into its component parts.

Table 3--Net transport of water at Bikini in trade-wind season per tidal cycle

Tide stage	Duration per cycle	Flow			
		Over reefs	Through channels	Through passes	Total
	hr	m^3	m^3	m^3	m^3
High	0.5	21,000 - 1,000	- 12,000	- 11,000	- 3000
Ebb	5.8	175,000 - 28,000	-215,000	-697,000	-765,000
Low	0.5	3000	- 12,000	- 15,000	- 24,000
Flood	5.2	172,000	256,000 - 71,000	429,000	786,000

Net inflow, 786,000 m^3/day; net outflow, 792,000 m^3/day
Positive values denote inflow; negative values, outflow

Table 4--Total transport of water at Bikini in trade-wind season per tidal cycle

Flow over or through	Inflow	Outflow
	m^3	m^3
Reefs	21,000	1000
	175,000	28,000
	3000	
	172,000	
Channels	256,000	12,000
		215,000
		12,000
		71,000
Passes	429,000	11,000
		697,000
		15,000
Sums	1,056,000	1,062,000

Table 5--Volumes of water transported at Rongelap per tidal cycle

Through	Flood	Ebb
	m^3	m^3
Northeast Pass	94,000	- 60,000
Gogan Pass	20,000	- 20,000
Enybarbar Pass	200,000	- 100,000
South Pass	630, 000	- 374,000
Pigen Pass	44,000	- 35,000
Enigan Pass	35,000	- 30,000
Kaeroga Pass	200,000	- 200,000
West Pass	-300,000	- 300,000
	923,000	-1,110,000
Northern reefs	180,000	140,000
Western reefs	- 40,000	- 65,000
	140,000	- 75,000
Total exchange	1,063,000	-1,054,000

The exchange budget for Rongelap is based upon more tenuous evidence consisting of a week of summer observations during which a steady state can be said to have existed. The measured contribution of each pass and estimated contribution of each reef section is shown in Table 5.

The total volume of Rongelap lagoon is approximately 47,000,000 m^3. Thus 2.2 per cent of the lagoon's volume is transported into and out of the lagoon during each tidal cycle. The value is remarkably close to that obtained for Bikini. The winter value may be roughly twice as great.

Secondary results--In the course of the circulation observations, large numbers of current poles were used in groups in combination with fluorescein dye which was trailed from the stern of an anchored skiff that marked the origin of the pole fields. Bundles of 30 poles were freed at the same time that the dye was released in the water to observe the dispersion of both indicators in response to horizontal diffusion in the surface layer of the lagoon. On the assumption that the dye was free of windage and represented the true progress of a given parcel of water in the current, it was found that the poles were unreliable. Only those current poles that were completely awash stayed with the edge of the dye. Others which protruded varying amounts drifted ahead of the dye as a result of their windage. Figure 6 gives the curves of the windage error for 16-ft 2 × 2 inch poles having various lengths exposed to a variety of wind forces. From these curves it appears that a standard current pole, which has 12 inches of its 15 ft of length exposed in air [HAIGHT, 1938, p. 17], is capable of ten per cent error in a 20-knot wind. The addition of pennants, targets, and other aids to visibility increases the possibility of error many-fold.

The dye trails between the skiff and the pole fields frequently took on a sinusoidal shape much exaggerated in Figure 7. The period of the dye wave in Bikini Lagoon was 1500 sec, too long to be

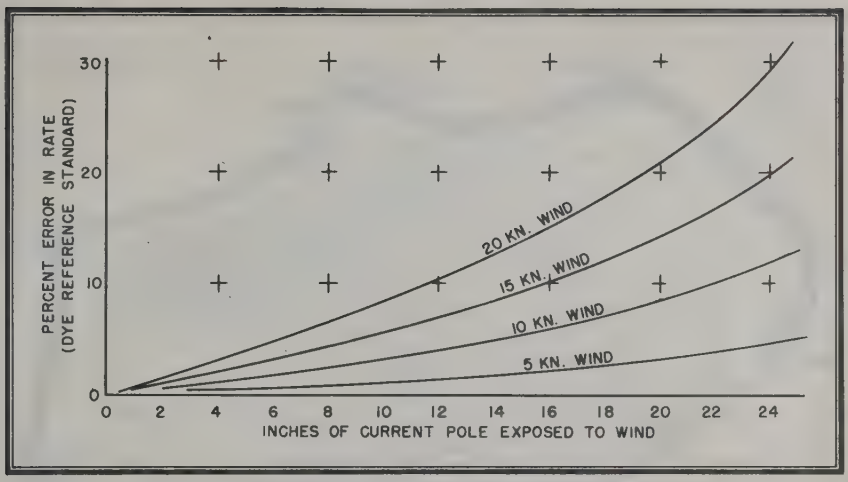

Fig. 6--Windage of 16-ft, 2 × 2-inch current poles

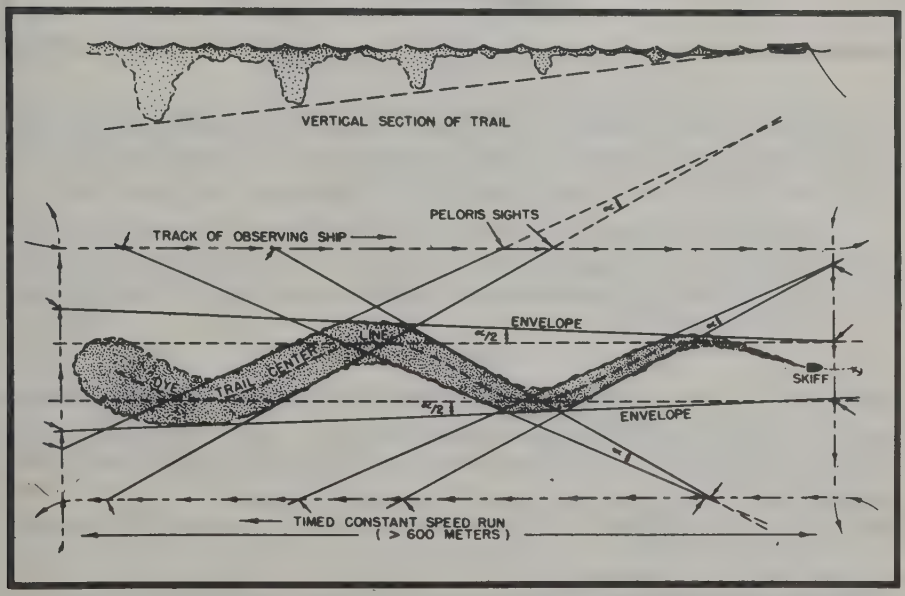

Fig. 7--Operation plan used for dye drift experiments and the nature of the results

accounted for by the yawing of the skiff on her anchor rode. The wave length of the trail was usually of the order of 300 m and the amplitude 25 m. The angles α marked on the figure to represent the divergence of the dye in the trail, and also the divergence of the trail envelope, were found to be equal and to have values ranging from 08° to 14°. This identity indicates that the center line of the trail had constant amplitude and period and that the divergence of the trail and of its envelope both result from eddy diffusion. The angles of divergence were independent of the speed of the surface current but closely related to the amount of shear in the upper 15 ft of the surface layer. The shear was observed qualitatively by means of weighted dye-packs which left a vertical dye trail in the water. The vertical section of the dye trail was seen to have downward

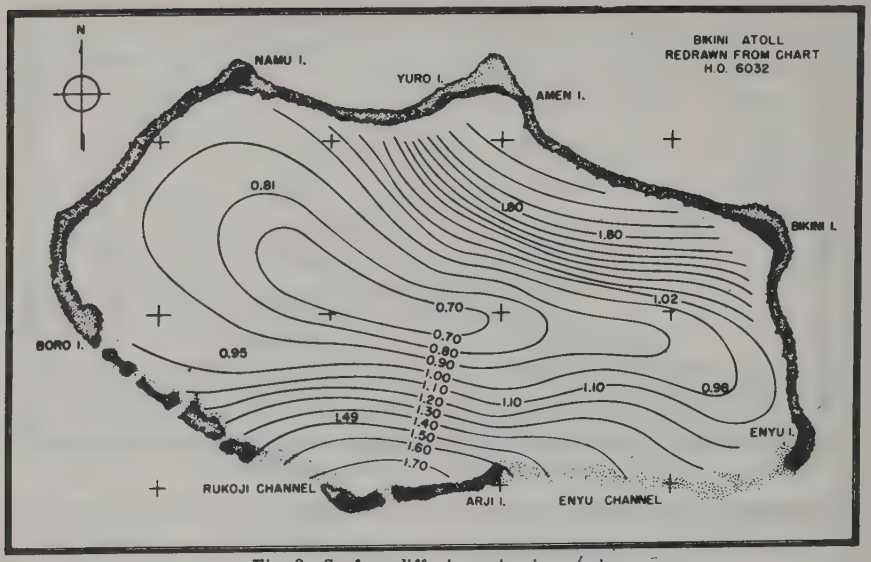

Fig. 8--Surface diffusion rates in m/min

developments at approximately regular intervals which were deeper as one approached the distal part of the trail. It was impossible to fix the positions of the downward developments with respect to the sinuosity of the trail because the latter could only be seen from the ends of the trail while the former could only be seen from the sides. Analogous patterns have been observed in airborne smoke trails over the sea surface [WOODCOCK and WYMAN, 1947, plates 2 and 4].

Ten experiments with dye trails and poles were performed at Bikini to measure the rate of lateral diffusion on the surface. These data are plotted in Figure 8 and lines of equal diffusion rate drawn through them, calculated as the rate of expansion in m/min of an equivalent dyed spot of water. The vales are larger wherever the horizontal component of the secondary circulation of the lagoon is most active.

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(Manuscript received May 13, 1948; presented at the Twenty-Eighth Annual Meeting, Washington, D. C., April 28, 1947; open for formal discussion until May 1, 1949.)

Contribution No. 423

Reprinted from JOURNAL OF METEOROLOGY, Vol. 5, No. 3, June, 1948, pp. 113–115
Printed in U. S. A.

IVORY'S PSYCHROMETRIC FORMULA AND THE CONCEPTS OF EQUIVALENT TEMPERATURE AND WET-BULB TEMPERATURE

By R. B. Montgomery

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(Manuscript received 24 December 1947)

This historical note is intended to bring to light certain outstanding but commonly unappreciated events in the development of psychrometry and of the concepts of the equivalent temperatures and the wet-bulb temperatures. A summary of the literature, which is exceptionally extensive in these subjects, is not attempted. The development of psychrometry has been summarized by Bongards (1926, pp. 132 ff.), whose book brought Ivory's work to the writer's attention. Various papers on equivalent temperature have been summarized by Robitzsch (1939).

Present state of the basic theory.—"*The wet-bulb temperature* may be defined as the lowest temperature to which air may be cooled by evaporating water into it" (Hewson and Longley, 1944, p. 60). Necessary additional conditions are that water at the wet-bulb temperature[2] is supplied to the air and that the process is adiabatic and isobaric (the total pressure is constant; the partial pressures change). The wet-bulb temperature agrees very closely with the temperature of a ventilated wet bulb (the ventilation must exceed 3 or 4 m s^{-1} according to Middleton, 1943, pp. 96, 100).

Symbols are defined as follows:

T = absolute temperature
T_w = absolute wet-bulb temperature
L_w = latent heat of vaporization at the wet-bulb temperature
w = mixing ratio
w_w = saturation mixing ratio at the wet-bulb temperature and actual pressure
c_{pd} = isobaric specific heat of dry air
c_{pv} = isobaric specific heat of water vapor.

It follows from the definition of wet-bulb temperature that a mass M of dry air and a mass Mw of water vapor are imagined to cool from T to T_w and a mass $M(w_w - w)$ of water to evaporate at the temperature T_w. The enthalpy of the dry air decreases by $Mc_{pd}(T - T_w)$, and that of the water vapor decreases by $Mwc_{pv}(T - T_w)$. The enthalpy of the added water

[1] Contribution No. 423.

[2] Van Mieghem (1941) specifies that the added water has the same temperature as the air, a condition which cannot in practice be achieved so easily and accurately. The method and result given here depend only on the first law of thermodynamics for a closed system and are essentially the same as the common ones first given by Ivory and later, for instance, by Brunt (1939, p. 86). Van Mieghem's method and result are no more rigorous but are far more complicated. Consequently his opening sentence, criticizing previous theories, does not seem to be justified.

increases by $ML_w(w_w - w)$. Since the process is adiabatic and isobaric, the total change in enthalpy is zero. Hence,

$$(c_{pd} + wc_{pv})(T - T_w) = L_w(w_w - w), \quad (1)$$

the basic and complete form of the *psychrometric formula* (for a ventilated psychrometer).

Ivory's formula.—Before being simplified, the formula derived by the Scottish mathematician Ivory (1822, p. 85) is

$$\frac{p-e}{p-e_w} = \frac{5e + \{240c_{pd} \times \frac{1}{30}(p-e) + 5ec_{pv}\}(T-T_w)/L}{5e_w}, \quad (2)$$

where the original symbols have been replaced with symbols of identical significance and with p for total pressure, e for vapor pressure, and e_w for saturation vapor pressure at the temperature of the wet bulb, and where, of course, T_w is used to represent the temperature of the wet bulb—'wet-bulb temperature' being a much more recent concept. On substitution of

$$w = \tfrac{5}{8}e/(p - e) \quad \text{and} \quad w_w = \tfrac{5}{8}e_w/(p - e_w),$$

(2) becomes

$$(c_{pd} + wc_{pv})(T - T_w) = L(w_w - w). \quad (3)$$

This formula is identical with (1), except that Ivory did not specify that the latent heat should correspond to the temperature of the wet bulb. Formula (3) is more complete, in spite of this exception, than Normand's (1921) widely cited formula. To Ivory, whose name is seldom mentioned in psychrometry, is due the credit for first publishing the psychrometric formula in essentially complete form.

Equivalent temperature.—The first published use of equivalent temperature was by Schubert (1904), who called it "ergänzte Temperatur." Knoche (1905) was the first to use, in print, the term "äquivalente Temperatur" (his last paper on equivalent temperature was published posthumously in 1945). Both Schubert and Knoche credit the concept to Bezold, who did not mention it in any publication. Credit for the introduction of equivalent temperature can therefore properly be divided between Bezold, Schubert, and Knoche.[3]

The definitions given by Schubert and Knoche are not precise but amount to saying that the equivalent temperature of air is the temperature the dry air present would achieve on being warmed with the heat latent in the water vapor. Both authors recognized equivalent temperature as a measure of total heat (now called 'enthalpy').

Wet-bulb temperature.—The concept of wet-bulb temperature as a property of air, rather than as the temperature of an insulated, wet surface, was introduced by Carrier (1911), who (p. 1014) stated that "the true wet-bulb temperature of the air depends entirely on the total . . . heat" (enthalpy). This concept formed the subject of subsequent publications by Prött (1913: see Linke, 1922), Schubert (1915), and Normand (1921).

The relation between wet-bulb and equivalent temperatures was demonstrated by Schubert (1915). Later Normand (1921) defined the *equivalent temperature* of a sample of air as the temperature of dry air at the same pressure and wet-bulb temperature. According to this definition and (1), the relation between equivalent temperature T_e and wet-bulb temperature T_w is both exact and simple:

$$T_e = T_w + L_w w_w / c_{pd}. \quad (4)$$

Equivalent potential temperature.—For this name and concept we owe credit to the independent publications of Normand (1921) and Schmidt (1921). However, Normand's definition made the quantity not precisely conservative, and Schmidt gave no clear definition. According to a more acceptable definition, *equivalent potential temperature* "is the equivalent temperature attained by a mass of air brought adiabatically to a standard pressure" (Brunt, 1939, p. 95).

Wet-bulb potential temperature.—Introduced by Normand (1921), *wet-bulb potential temperature* was defined as "that wet bulb temperature which the air assumes when it is brought adiabatically to standard pressure."

Other temperatures by the same names as those above have been defined for special purposes and are discussed in modern meteorological texts. Different temperatures under the same name usually differ only slightly in value; however, an 'equivalent temperature' introduced into hygiene by Dufton (1933) bears no close relation to the established family of equivalent temperatures used by meteorologists.

[3] It is of interest to note that Bezold shares with Helmholtz the credit for potential temperature; the concept was first used by Helmholtz (1888), but the term "potentielle Temperatur," subsequently suggested by Helmholtz, was first published later in the same year by Bezold (1888). Of the many fictitious temperatures used in meteorology, the first was virtual temperature, introduced by Guldberg and Mohn (1876).

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Contribution No. 425

Reprinted from Ecology, Vol. 29, No. 1, January, 1948
Printed in U. S. A.

THE NUTRITIONAL VALUE OF MARINE ZOOPLANKTON WITH A CONSIDERATION OF ITS USE AS AN EMERGENCY FOOD [1]

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Introduction

It has long been realized that the waters of the earth contain a larger total amount of living organisms than does the land because of their much greater extent, and therefore offer a larger potential food supply for man and other terrestrial organisms. This aquatic food resource has been drawn upon by man chiefly in the form of his catch of fish, mollusks, and the higher crustacea. These animals form only a small part of the life in the sea. Furthermore, such organisms are either at the end or near the end of the aquatic food chains. From an understanding of the dynamics of production, we know that organisms near the beginning of the food chains are produced at a higher rate and their standing crop is often greater (Clarke, '46). In an effort to improve the efficiency with which we use the food resources of our marine and inland waters, we should therefore consider whether we could not utilize to some extent organisms near the base of the production pyramid, such as the plankton,[3] as well as those at its peak. Only a small fraction of the populations at the lower trophic levels actually go into the formation of the fish and other animals now harvested by man.

The possibility has been discussed previously of obtaining plankton of a suitable nature and in sufficient abundance to serve as a source of food for man or domestic animals (Clarke, '39; Hardy, '41; Juday, '43; and Shropshire, '44).[4] However, practically no information has been available on the nutritive value which could be derived from the plankton by terrestrial animals, and more information was needed on the variations in the availability and chemical composition of the plankton before any general conclusions could be reached. The present investigation was undertaken to secure pertinent data on these points. The nutri-

[1] This investigation was made for the Woods Hole Oceanographic Institution under contract with the Air Material Command (Aero-medical Laboratory) of the Army Air Force, Wright Field, which has given permission for its publication. The opinions presented here are those of the authors and do not necessarily reflect the official opinion of the Army.

[2] Contribution No. 425.

[3] Since the preparation of this report we have been informed by Dr. S. P. Chu of the National University of Shantung that along the northern coast of China a "shrimp paste" is made from the plankton and this serves as a "main accessory food" for the poor people all over China, especially in winter. In preparing the paste, salt is added which enables the material to keep indefinitely, and an oil is extracted which is sold separately. Whether the organisms which form this paste can be compared with the general offshore plankton is not known. Various kinds of small marine crustacea are eaten in the Scandanavian countries.

[4] Since the preparation of the present paper a report has appeared on the use of plankton as food during an experimental raft drift of several thousand miles westward from Peru (Heyerdahl, 1947). Plankton obtained by towing a regular silk plankton net was found by four members of the six-man expedition to be "exceptionally palatable" either raw or cooked and to "satisfy hunger." No information is given, however, as to (1) the amount of plankton eaten per man per day, (2) the amount of other food also eaten, and (3) the amount of fresh water taken with the plankton.

tive value of plankton for rats was determined by direct feeding trials. In addition, tests were made of the feasibility of the use of marine plankton as a source of food under emergency conditions at sea, as for example, by life raft occupants.

In the present investigation tests were confined to the zooplankton which is retained by a coarse plankton net. Although the standing crop of diatoms or of flagellates is sometimes greater than that of the larger plankton, the difficulty (Clarke, '37) and possible danger (see below) of obtaining the marine phytoplankton and nannoplankton in sufficient quantities would probably make the use of these forms impractical. The findings are discussed in relation to the general problem of the direct and indirect use of plankton by man.

Detailed information on the abundance and variability of plankton in a rich marine area was obtained from the eleven surveys of Georges Bank made from 1939 to 1940 (Clarke, Pierce, and Bumpus, '43). Direct tests on the amount of plankton obtainable from a life raft under known conditions of abundance were made from Woods Hole during July, 1945. Tests on the feeding of plankton to rats were conducted at Woods Hole during November, 1945. Chemical analyses of the plankton were carried out in the laboratories of Dr. A. M. Butler, Department of Pediatrics, Massachusetts General Hospital, and of Dr. Philip H. Smith, Agricultural Experiment Station, Amherst, Massachusetts. The authors are indebted for assistance to Dr. A. D. Bajkov and Sergeant J. B. Chadwick of the Air Technical Serv-

TABLE I. *Zooplankton volumes for Georges Bank region*

Volumes were obtained by displacement measurement of drained plankton and are expressed as cubic centimeters of plankton per cubic meter of sea water. Plankton taken by plankton sampler with No. 2 silk net. Nineteen hauls in which diatoms comprised an important fraction were omitted; Numbers of hauls on which values are based ranged as follows: Shallow, 21–52; Second Depth, 21–36. Deep, 8–20. For further details see: Clarke, Pierce and Bumpus (1943).

Date	Value	Shallow	2nd Depth	Deep	Date	Value	Shallow	2nd Depth	Deep
Sept. 1939	Max.	4.4 cc.	1.3* cc.	— cc.					
	Min.	.1	.07*	—					
	Av.	.9	.4*	—					
Jan. 1940	Max.	1.8	.5	1.2					
	Min.	.06	.05	.04					
	Av.	.3	.2	.1					
Mar. 1940	Max.	3.6	3.7	1.1	Mar. 1941	Max.	1.0 cc.	0.4 cc.	0.5 cc.
	Min.	.1	.03	.03		Min.	0.1	0.03	0.04
	Av.	.6	.6	.2		Av.	0.3	0.2	0.1
Apr. 1940	Max.	5.9	3.1	3.7	Apr. 1941	Max.	6.2	7.3	0.8
	Min.	.1	.05	.1		Min.	0.2	0.1	0.1
	Av.	1.2	.9	.6		Av.	1.6	1.2	0.3
May 1940	Max.	3.4	4.1	3.8	May 1941	Max.	6.4	3.1	2.6
	Min.	.3	.2	.1		Min.	0.5	0.3	0.1
	Av.	1.4	1.0	0.8		Av.	1.9	1.2	0.7
June 1–8, 1940	Max.	5.3	4.9	1.5	June 1941	Max.	7.2	5.5	5.4
	Min.	.08	.04	.04		Min.	0.4	0.3	0.1
	Av.	1.7	1.2	.5		Av.	1.9	1.8	0.9
June 19–27, 1940	Max.	10.1	4.0	3.6					
	Min.	.06	.08	.04					
	Av.	1.7	1.1	.5					

* 2nd Depth and Deep hauls combined.

ice Command, and to Dr. Y. H. Edmondson, Mr. G. C. Whiteley, and Mr. D. F. Bumpus of the Woods Hole Oceanographic Institution. Dr. Butler kindly assisted in the interpretation of the results from the viewpoint of the water balance of the body.

Abundance and Availability of Plankton

On the basis of a four-year survey of the relatively rich coastal area between Cape Cod and Chesapeake Bay, Bigelow and Sears ('39) reported that the average concentration of zooplankton in the upper water layers during the season of maximum production was about 0.5 to 0.8 cc./m³. Comparison with other investigations showed that the plankton of European waters was little, if any, richer. There is no evidence that the plankton of the Pacific Ocean in general is significantly more abundant than that of the Atlantic. Polar seas have been reported to be richer in plankton than oceanic areas of lower latitude (Bajkov, '45).

A more intensive survey of the abundance of zooplankton and of its variation was made during eleven cruises to Georges Bank, off Cape Cod, between September, 1939 and June, 1941. On each cruise a network of stations was occupied and the abundance of the zooplankton accurately determined by means of Plankton Samplers (Clarke and Bumpus, '40) equipped with No. 2 silk nets (22 strands/cm.). The volumes of drained plankton (measured by displacement) varied greatly both in time and in space (table 1). An example of the variation from station to station during one cruise is given in figure 1 which represents a period of high plankton abundance. However, it is obvious that the area as a whole is generally richer than that reported by Bigelow and Sears

Fig. 1. The abundance of zooplankton in cubic centimeters (displacement volume) per 10 m.³ in the Shallow stratum (0–25 m.) on Georges Bank during the cruise of May 28–June 4, 1941.

TABLE II. *Locations and abundance of plankton for tests with life rafts*

Test	Date	Location	Wind	Sea	Plankton abundance
1	July 20, 1945	Vineyard Sound off Quicks Hole	5 knots	Smooth	0.72 cc./m.^{3}
2	July 26, 1945	Vineyard Sound off Tarpaulin Cove	10	Slight	1.12
3	July 27, 1945	Cape Cod Bay near Canal Whistle Buoy	18	Waves up to 4 ft.	0.45

and probably has as large a standing as any temperate area of comparable size. The amounts of zooplankton found here may therefore be taken as a rough measure of the maximum which could be expected in temperate oceanic regions.

A comparison of the plankton catches from the three strata into which the water was divided (for procedure see Clarke, Pierce, and Bumpus, '43) reveals the fact that in most cases the animals were most abundant in the "Shallow" stratum, which extended from 0 to 25 m. There would thus be no advantage in attempting to obtain plankton in quantity from the deeper layers. For the "Shallow" stratum the average size of the hauls for each cruise ranged from 0.3 to 1.9 cc. of plankton per cubic meter of sea water. Out of the 367 individual "Shallow" hauls in which zooplankton predominated and from which the averages of table I are taken, only seven hauls had volumes greater than 5 cc./m^3. If 19 additional hauls are included which contained large amounts of diatom material, the number with total volumes greater than 5 cc./m^3. is increased to thirteen.

The amounts of plankton which could actually be obtained from a life raft by using a plankton net to replace the sea anchor, or drogue, were determined under conditions of plankton abundance comparable to the average richness of Georges Bank. The abundance of the plankton was determined by means of hauls with the Plankton Sampler made before and after the life raft tests (table II).

The plankton obtained from a Mark IV raft with one occupant (except in one case, as noted) under the conditions indicated and with nets of various materials are presented in table III. These tests showed that nets made of No. 2 silk were the most efficient for obtaining the existing type of plankton in which small copepods were the most abundant organism (see below). With the coarser nylon netting a large proportion of the plankton was not retained and with the finer No. 10 silk the amount of water filtered was reduced. Experience showed that with the strength of winds encountered in these tests the filtering rate of the nets could be increased by paddling or improvising a sail

TABLE III. *Amounts of plankton obtained from life raft*

Test	Diameter of net, cm.	Material	Threads per cm.	Duration of haul, minutes	Approx. speed, knots	Actual catch, cc.	Conditions
1	30	No. 10 silk	43	45	1	6.2	Improvised sail
	50	Nylon	8	60	—	1.0	Drifting
	50	Nylon	8	15	—	<1.0	2 men paddling
2	45	No. 2 silk	22	90	1	150	Improvised sail
3	45	No. 2 silk	22	30	0.5	20	Smaller improvised sail

TABLE IV. *Comparison of theoretical and actual catches of plankton*

	Test 1	Test 2	Test 3
Mesh of silk	No. 10	No. 2	No. 2
Area of net opening—m.²	.07	.16	.16
Volume filtered per mile—m.³	135	289	289
Volume of plankton/m.³ of water—cc.	0.4	1.0	0.3
Plankton obtainable per mile—cc.	54	289	87
Miles drifted in 24 hours	24	24	12
Plankton obtainable per 24 hours—cc.	1296	6936	1040
Actual catch, 24-hour basis—cc.	200	2400	960
Efficiency—per cent	15	34	92

to cause the raft to move more rapidly through the water.

Calculations of the amount of plankton which could be obtained on a 24-hour basis and of the efficiency of the nets are presented in table IV. The volume of water which would theoretically pass through an area equal to that of the opening of the net in 24 hours at the approximate rate of drift observed is determined as representing 100 per cent filtering efficiency for the net. The amount of plankton which would be obtained from this volume of water is then calculated from the plankton sampler data to provide a value for the maximum possible catch under the circumstances. This value is then compared with the actual catch on a 24-hour basis to obtain the filtering efficiency of the net as used.

The filtering efficiency of the No. 10 silk net was found to be low compared with that of the No. 2 silk net. The wide variation in the values for the latter are probably due in part to lack of precision in measuring the speed of the raft drift and in part to the larger amount of water which fails to enter the mouth of the net at the higher speed because of back pressure. There is thus a limit to the augmentation of the yield which is obtainable by increasing the rate of raft drift.

As the plankton accumulates in nets which are being towed, the filtering capacity is progressively reduced. This loss of efficiency may continue to some extent even if the catch is removed periodically because it is impossible to wash the mesh clean and because the thread itself swells and frays. There is thus some danger in projecting the results of tests of short duration for periods of 24 hours or more. For this reason the greatest value for the volume of the catch on a 24-hour basis of 2400 cc. may be higher than could actually be obtained.[5]

CHEMICAL ANALYSIS OF THE PLANKTON

A knowledge of the chemical composition of the plankton was desired as a means of calculating its potential nutritive value, and its possible effect on the water balance and salt balance of the body of the consumer. Plankton for chemical analysis was obtained during both the July and the November tests by towing several nets of No. 2 silk, 75 cm. in diameter, from the power vessel at 1 to 2 knots. In Test 1 (Sample A) aggregate towing time was equivalent to 1 net towed for 5⅓ hours and yielded 785 cc. of plankton. In Test 3 (Sample B) the towing time was equivalent to 5 hours and yielded 800 cc. of plankton. The towing time for the November collection was not recorded, but 1185 cc. of plankton were available for the analysis (Sample C).

[5] Since the preparation of the present paper, Heyerdahl (1947) has reported that during his experimental drift on a 45-foot raft under sail he obtained 2½ to 5 kg. of plankton per day for food using a silk plankton net of the same diameter and mesh as the one used in our tests No. 2 and No. 3. He states that the biggest catches were made in the cooler water near the Peruvian coast and that "copepods, pelagic crabs, and other crustaceans as well as eggs and larvae" were obtained. The coelenterates were always removed from the catch before eating as "they were found bitter."

TABLE V. *Species composition of the plankton*

The number of individuals of each species is given as per cent of the total

Sample A		Sample B	
Copepods		Copepods	
Centropages hamatus	75	*Arcartia tonsa*	69
Other species	15	Other species	7
Cladocera	7	Cladocera	16
Fish eggs	3	Fish eggs	8
Total per cent	100	Total per cent	100
Gastropods Fragments of algae Detritus	<1	No plant material or Detritus	

Identification and aliquot count of the organisms present in the July samples showed that crustacea greatly predominated both in volume and in number of individuals, as shown in table V. In each sample, a single species of copepod (individuals about 1 mm. in length) outnumbered all other organisms combined. The composition of the plankton obtained in November was about 95 per cent copepods (largely *Centropages* sp.) with small percentages of other crustacea, worms, pelecypods, and fish larvae. In these samples for analysis the plankton was predominately crustacean and was therefore typical of the usual oceanic plankton.

Each sample was divided into three parts which were treated as indicated at

TABLE VI. *Weights and chemical composition of plankton samples*

Treatment of Subsamples:

A-1: Drained, weighed wet, dried at 65° to 85° C. for about 65 hours, and weighed dry.
A-2: Drained, washed by pouring 600 cc. of fresh water over it, allowed to drain, weighed wet, dried, and weighed dry.
A-3: Drained, excess water squeezed out by hand through netting with moderate pressure, weighed wet, dried for 17 hours, placed in desiccator for 48 hours, weighed dry.
B-1: Drained, bottled and placed in refrigerator.
B-2: Drained, excess water squeezed out by hand, bottled and placed in refrigerator.
B-3: Drained, squeezed as before, stirred in 2 liters of fresh water for about 3 minutes, drained and squeezed again, bottled and placed in refrigerator.
C-1: Drained for 20 minutes, weighed wet, placed in oven and dried at 80° C. for 189 hours and weighed dry.
C-2: Washed with 1000 cc. of distilled water, drained 20 minutes, weighed wet, dried at 80° C. for 188 hours and weighed dry.
C-3: Drained for 20 minutes, squeezed in No. 2 silk netting with moderate pressure, weighed wet, dried at 80° C. for 188 hours and weighed dry.

Sample	Treatment	Volume, cc.	Wet wt., grams	Dry wt., grams	N	P	Ca	K	Mg	Na	Cl
					Milligrams per gram dry weight						
A-1	Drained	260	261	29.5	90	8.5	5.2	6.6	8.4	64	125
A-2	Washed-drained	260	272	24.7	100	9.2	3.8	3.9	4.9	30	53
A-3	Drained-squeezed	260	147	21.3	98	8.3	3.6	3.9	6.4	44	82
B-1	Drained	250	214*	20.4	77	13.9	—	4.7	—	—	139
B-2	Drained-squeezed	250	166	21.4	91	11.7	—	—	—	—	89
B-3	Squeezed-washed-squeezed	250	126	13.2	105	10.0	—	—	—	—	25
C-1	Drained	393	395	38.9	84	7.6	9.6	14.2	12.9	83	147
C-2	Washed-drained	392	372	29.7	95	7.6	10.0	10.1	7.8	36	58
C-3	Drained-squeezed	400	224	33.6	90	7.6	10.0	10.0	9.6	53	92

* Some of liquid lost in transit.

the top of table VI to ascertain to what extent adhering salt water and/or salt body fluids could be eliminated from the plankton by procedures which might conceivably be practicable for life-raft occupants. In the case of each part the plankton was first allowed to drain on a piece of the No. 2 silk netting and its volume measured by displacement.

The chemical analyses of Samples A and B were carried out at the Massachusetts General Hospital and that of Sample C at the Massachusetts Agricultural Experiment Station (table VI). It is clear that the analyses of the three samples are in very good general agreement and the subsamples which received the same treatments show comparable differences. The amount of nitrogen present was similar for all three samples and the protein content may be calculated from it. No explanation is apparent for the greater amount of phosphorus in Sample B than in the other samples. Of the other elements analyzed the chlorine and the sodium were the most abundant in all cases.

A more detailed analysis of the constituents of the plankton from the nutritional viewpoint was carried out for Sample C (table VII). The percentage of protein in the dried material which ranged from 52 to 59 per cent in this sample (and from 46 to 63 per cent in the other samples) agrees closely with previous reports (see below), but the proportion of fat and ash is lower. The sodium chloride was reduced from about 22 per cent in the drained subsample to about 14 per cent in the squeezed subsample, and to about 9 per cent in the subsample which was washed with fresh water.

The effects of the different treatments of the subsamples are most clearly shown when the data are placed on a relative basis, as in tables VIII and IX. The specific gravity of the drained plankton is obviously very nearly 1 since the wet weight in grams is essentially equal to the volume in cubic centimeters. Squeezing the plankton reduced the wet weight of the sample by one-third to one-half. The weight of dry material obtainable from 100 cc. of plankton was similarly reduced from 11.0 g. for a sample which was simply drained to 5.3 g. for the sample which was squeezed, washed, and squeezed again. The dry weight of the plankton varied from 8 to 15 per cent of the wet weight depending upon the treatment.

The reductions in dry weight following washing and squeezing are presumably

TABLE VII. *Nutritional constituents of plankton*

Components of Sample C expressed as per cent of total weight of sample dried at 80° C.

	Subsample C-1 (drained)	Subsample C-2 (washed-drained)	Subsample C-3 (drained-squeezed)
Protein (N × 6.25)	52.6	59.1	56.2
Fat	1.4	4.2	4.1
Total ash	32.9	19.4	24.1
Carbohydrate (by difference)	13.1	17.3	15.6
Total per cent	100.0	100.0	100.0
Insoluble ash	2.7	3.9	3.5
Chlorine	14.9	5.8	9.2
Chlorine (Est. as NaCl)	24.2	9.6	15.2
Sodium	8.3	3.6	5.3
Sodium (Est. as NaCl)	21.1	9.1	13.4
Phosphorus	0.76	0.76	0.76
Potash	1.42	1.01	1.00
Calcium	0.96	1.00	1.00
Magnesium	1.29	0.78	0.96
Sulphur	0.71	0.46	0.55
Carotene—p.p.m.	3	4	4

TABLE VIII. *Relative compositions of plankton following various treatments*

Sample	Treatment	Wet weight of 100 cc., grams	Dry weight of 100 cc., grams	Dry weight / Wet weight per cent	Protein of 100 cc., grams	Protein* per cent dry weight	Protein* per cent wet weight	Chloride per cent dry weight	Chloride† per cent wet weight
A-1	Drained	100	11.0	11.0	5.9	54	5.9	12.5	1.4
A-2	Washed-drained	105	9.5	9.1	5.8	60	5.5	5.3	0.5
A-3	Drained-squeezed	57	8.2	14.0	4.7	59	8.3	8.2	1.1
B-1	Drained	86**	8.2	9.5	3.8	46	4.4	13.9	1.3
B-2	Drained-squeezed	66	8.6	13.0	4.7	55	7.1	8.9	1.2
B-3	Squeezed-washed-squeezed	50	5.3	10.6	3.3	63	6.7	2.5	0.25
C-1	Drained	101	9.9	9.9	4.9	50	4.9	14.7	1.6
C-2	Washed-drained	95	7.6	8.0	4.4	57	4.6	5.8	0.5
C-3	Drained-squeezed	56	8.4	15.0	4.5	54	8.1	9.2	1.4

* Assuming 6 grams protein for 1 gram nitrogen.
† Chloride in sea water from Vineyard Sound (Salinity = 32°/00) = 1.8 per cent.
** Liquid lost in transit affects figures for this subsample.

TABLE IX. *Relative abundance of elements*
Adjusted to sodium = 100 grams

Element	A-1 Drained	A-2 Washed	A-3 Squeezed	C-1 Drained	C-2 Washed	C-3 Squeezed	*Calanus** (copepod)	Whole fish*	Sea water*
Chlorine	188.0	171.0	191.0	178.0	161.0	174.0	194.0	180.0	
Sodium	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Magnesium	12.9	15.8	14.5	15.5	21.6	18.1	5.6	36.0	12.1
Potassium	10.1	12.6	8.9	17.1	28.0	18.9	53.7	383.0	3.6
Calcium	8.0	12.3	8.2	11.6	27.8	18.9	7.4	52.0	3.8
Phosphorus	13.0	29.8	18.9	9.2	21.1	14.3	24.1	256.0	0.0001
Nitrogen	138.0	322.0	222.0	101.0	264.0	170.0	280.0	1276.0	0.001
Nitrogen/ Phosphorus	10.6	10.8	11.7	11.0	12.5	11.9	11.6	5.0	—
Chlorine/ Nitrogen	1.4	0.53	0.86	1.8	0.63	1.0	0.69	—	—
Magnesium/ Nitrogen	0.094	0.049	0.065	0.15	0.082	0.11	0.020	0.028	—

* From Table 50, Sverdrup, Johnson, and Fleming (1942).

due chiefly to the elimination of the salts contained in the adhering salt water, but some body fluids may have been pressed out as well. A certain amount of nitrogenous material was also lost as a result of squeezing since the amount of protein obtained from 100 cc. of plankton was reduced from 5.9 g. and 4.9 g. in Samples A-1 and C-1 respectively to 4.7 g. and 4.5 g. in Samples A-3 and C-3 which were squeezed. From 100 cc. of Sample B-3, which was subjected to the double squeezing process, only 3.3 g. of protein was obtained. Since the percentage of protein in the dry material was greater for the squeezed than for drained subsamples whereas the reverse was true in the case of the chloride, it is obvious that the loss of chloride was relatively much greater.

The chloride present in the subsamples of the plankton following the various treatments designed to eliminate salt water composed from 2.5 per cent to 14.7 per cent of the dried material, and from 0.25 per cent to 1.6 per cent of the wet

weight. Since sea water of a salinity of 32 per cent (as in Vineyard Sound) contains 1.8 g. of chloride per 100 cc., it is evident that in consuming drained plankton, about 80 per cent as much chloride would be taken in as if an equal weight of sea water were drunk. This figure is reduced to about 70 per cent for squeezed plankton, to as little as 30 per cent for washed plankton, and to 15 per cent following the double squeezing and washing process.

Other solutes were also reduced in amount by the squeezing and especially by the washing treatment. The differences in the amount of the reduction for the commoner ions may be observed from their relative abundance in the subsamples as shown in table IX. There is little consistent change in the ratio of chloride to sodium but magnesium tended to become relatively more abundant following the squeezing and the washing processes. When compared with nitrogen, which may be taken as an index of the protein present, it is seen that chloride is reduced relatively to about one-third by the washing process and magnesium to about one-half.

The relative abundance of elements in our material may also be compared with the ratios reported for the copepod, *Calanus,* for whole fish, and for sea water (table IX). We have no information as to the manner in which the *Calanus* material was treated before analysis, but it is clear that the ratios of chlorine, calcium, phosphorus, and nitrogen to sodium are similar to our values. The value for magnesium is much lower and the value for potassium is much higher. The analysis for fish shows all ratios considerably higher, and indicates that sodium is relatively low. When compared with sea water, our drained subsamples (A-1 and C-1) exhibit a close agreement for the ratios of chlorine and magnesium to sodium, but potassium and calcium are considerably higher. The relative abundance of magnesium increased noticeably for the squeezed and washed samples. The ratio of magnesium to potassium both in sea water and in the plankton is much higher than in the body fluids of man. The ratio of nitrogen to phosphorus in the samples of plankton was somewhat higher than that previously reported (Sverdrup, Johnson, and Fleming, '42, table 52).

We may draw the following conclusions from the foregoing analyses and their relative differences. If it is found that the salt content of the plankton is of no consequence to the consumer, then the largest amount of protein per unit volume of plankton catch will be obtained by eating the drained material without further treatment. If, however, it is desirable to eliminate as much of the salt as possible, the plankton should be squeezed, or, if possible, washed with fresh water. Squeezing may cause the loss of some 20 per cent of the protein, but a larger percentage of the salts will be lost. Washing causes little loss of protein and about 65 per cent of the chloride and 55 per cent of the magnesium will be removed (or more with the double squeezing and washing process). The concomitant increase in the ratio of magnesium to sodium must be kept in mind as of possible importance in the salt balance of the consumer.

Feeding Experiments with Rats

The foregoing chemical analysis gives maximum figures for the nutritive content of plankton but yields no information on the portion of the plankton which could actually be assimilated by man or other terrestrial animals, nor on any possible harmful effects. Preliminary experiments were therefore undertaken on the effect of feeding plankton to rats. Both adult and weanling white rats (Wistar stock) were used for these tests and were maintained in Dawson type cages, loaned by the Biological Laboratories of Harvard University. One or two adult rats, or one to three weanlings, were kept in each cage.

The plankton used for feeding was obtained from Vineyard Sound and most of

it was frozen at $-18°$ to $-20°$ C. immediately upon reaching the laboratory, but supplementary tests were conducted with fresh and with cooked plankton. The plankton fed the experimental animals was squeezed with moderate pressure in No. 2 silk netting to remove excess sea water. Tests showed that the dry weight of this material was about 14 per cent of the wet weight. Diet mixtures were prepared on the basis of the dry weight of the plankton. Control food consisted of Purina-Growena meal and Purina dog chow checkers. The type of plankton used was found to have an average energy content of about 4 calories per gram of dry weight (see below) which was assumed to be comparable to the energy content of the control food.

The main series of experiments consisted of comparing the growth rates of rats fed on full and partial diets of control food with those fed on plankton alone, and on diets of $\frac{2}{3}$ and $\frac{1}{3}$ plankton with the balance made up with control food. The average intake of control food which resulted in the maximum growth rate of weanling rats was found to be 13 grams of Purina-Growena meal per rat per day. With more supplied, considerable quantities were left in the cage; with less supplied, the growth curve fell off. In all cases the animals had access to an adequate supply of water from bottles in which the consumption could be estimated.

The growth rate of weanling rats fed on a full diet of meal was first compared with the rates for animals fed on a diet of $\frac{2}{3}$ meal plus $\frac{1}{3}$ plankton and for animals fed on a deficient diet of $\frac{2}{3}$ meal and no plankton. The rats consumed 32 g. of wet squeezed plankton mixed with 8.5 g. of meal per rat per day which was calculated to be equivalent to 4.5 g. dry plankton plus 8.5 g. of meal. Although the growth of the rats fed plankton was more irregular than that of the controls, the average rate for the former over the 13-day period of the experiment was essentially the same as for the controls (fig. 2). Since the growth of the rats fed $\frac{2}{3}$ of the normal amount of meal

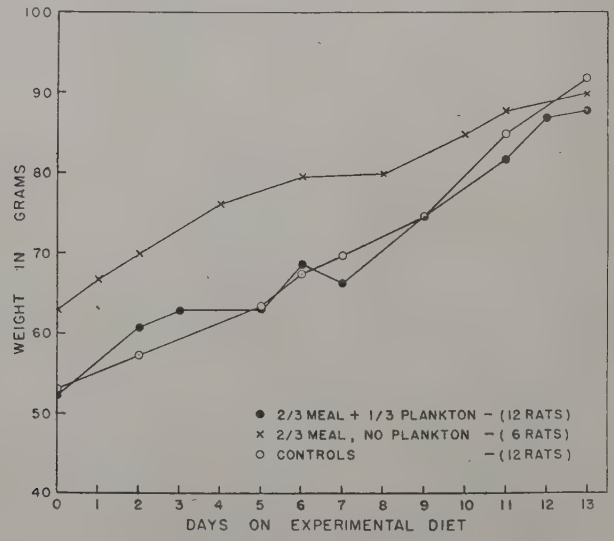

FIG. 2. Growth curves of weanling rats fed on the indicated diets. The average values for each group of animals are plotted.

alone was definitely depressed, it is clear that some nourishment was derived from the plankton which was added to the diet.

In the next experiment the growth of weanling rats fed on a diet of ⅓ meal plus ⅔ plankton was compared with that of rats on a diet of ⅓ meal and no plankton. The animals in the first group received 60 g. of wet squeezed plankton (equivalent to 8.5 g. dry plankton) plus 4.5 g. of meal per rat per day. The rats in this group actually consumed only about ⅔ of the food which was offered them although the full amount was theoretically required for their nutritive requirements. The growth of these animals stopped abruptly on the first day on which they were placed on the diet with plankton. The rats, nevertheless, succeeded in maintaining their original weight for 7 days. The animals of the second group, which received no plankton to supplement their ⅓ diet of meal, lost weight during the same period (fig. 3). This result again shows that some nourishment is derived

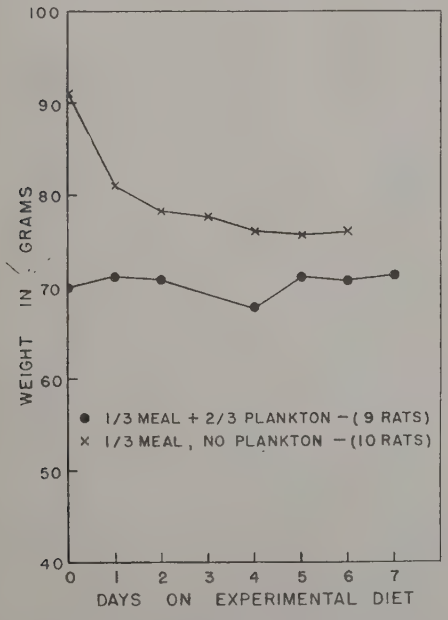

FIG. 3. Weight records of weanling rats fed on the indicated diets.

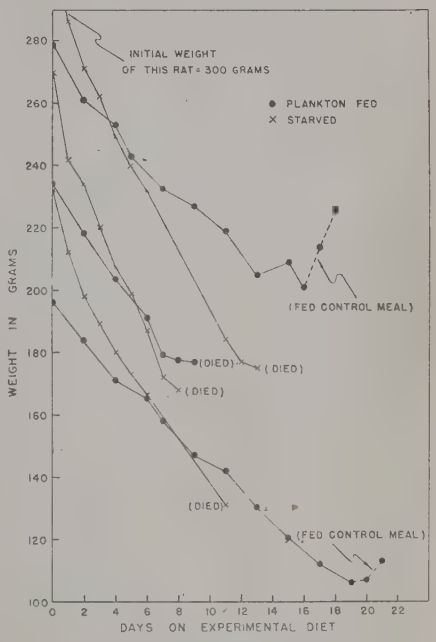

FIG. 4. Weight records of adult rats fed on plankton and of starved rats.

by the rats from plankton, but when as much as ⅔ of the diet is composed of plankton, normal growth does not take place. The inadequacy of the diet with plankton may be due partly to the refusal of the rats to eat a sufficient amount. That it is also due in part at least to their inability to assimilate from the plankton a sufficiently large fraction of the energy which it contains is shown by the fact that these rats which consumed ⅔ of their ration of mixed food did not do as well as those in the previous experiment which ate ⅔ of a ration composed entirely of control food.

When rats were fed a diet consisting entirely of plankton, they not only failed to grow, but lost weight rapidly and eventually died. They survived for a longer period, however, than rats which were given no food at all. Weanling rats showed a loss in weight of 5 to 10 grams after the first day on the plankton

diet and succumbed within four or five days. Adult rats fared better on plankton than did weanling rats. The longest survival times for adult rats on a full plankton diet were 18 and 19 days. Starved rats, of equivalent initial weights, given adequate water lived for a maximum of 13 days (fig. 4). The amount of plankton eaten by these rats was quite variable. The normal intake of control meal for adult rats maintaining a steady growth was found to be 20 g. per rat per day. Although 90 to 100 g. of wet squeezed plankton was offered per rat per day, adult rats on a full plankton diet consumed something less than 60 g. per day and this would be equivalent to only about 7 g. of dry plankton.

To reveal any possible adverse condition of the frozen and stored plankton which was used in the foregoing feeding tests, a further series of experiments was run with fresh plankton, brought into the laboratory just prior to feeding. Portions of this plankton were prepared simply by squeezing out the excess salt water, other portions were washed with distilled water, and others were washed and cooked for 20 to 30 minutes. Weanling rats were supplied with all the plankton prepared in these various ways which they would eat. The animals consumed an average amount of washed plankton equivalent to 12 g. of dried material per rat per day, but the average intake of cooked plankton was equivalent to only 8 g. of dry food, and that for fresh, unwashed plankton was equivalent to about 7 g. In spite of the fact that the amounts of plankton eaten under these circumstances in some cases approached the dry weight which would be adequate for control meal, all the rats lost weight rapidly and died after a few days (fig. 5). Weight loss was not quite as severe when washed and cooked plankton was fed as when untreated plankton was used. Animals fed on the latter material fared little, if any, better than those which were starved.

An ample supply of water was avail-

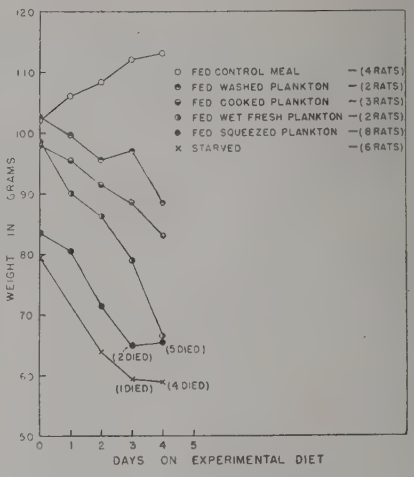

FIG. 5. Weight records of weanling rats fed on plankton treated as indicated.

able to the rats in all experiments at all times. The rats which were fed whole or partial plankton diets were found to consume on the average about the same quantity of water from the water bottles as the controls. The plankton-fed rats thus took in 86–90 g. of water with every 100 g. of squeezed plankton. Since this plankton contains about 86 per cent water, it is clear that the animals on this diet were taking in a larger total amount of water. Whether or not this larger total water intake was necessary was not determined. Theoretical aspects of the water balance of the body on a plankton diet are considered below.

Autopsies on plankton-fed rats showed few abnormalities. The most consistent and prominent symptom was a marked congestion of faecal material in the caecum and hind intestine. It is not clear whether the accumulation of indigestible matter was a contributing factor to death, or whether the general weakness and loss of muscle tone resulted in faulty elimination, incidental to the cause of death. The kidneys appeared quite normal. For a day or so prior to death the rats were anemic, weak, and lacked coordination.

These feeding experiments show in general that the rats will usually not eat an amount of plankton which would contain the requisite energy to permit normal growth. In those cases in which the rats were induced to eat an amount of plankton which would appear adequate or nearly so, on a dry weight basis, the animals nevertheless failed to grow. Only a small fraction of the energy contained in the food, therefore, appears to be utilized. Since the reduction in growth rate is immediate, a vitamin deficiency as the chief harmful effect is contraindicated. That some nutriment is derived from the plankton is shown by the longer survival of plankton-fed rats than starved rats, and by the lesser reduction in the growth rate for rats fed on a quantitatively deficient diet of meal plus plankton than for animals fed on the deficient meal diet alone.

Discussion

Variation in plankton type and abundance

In discussions of the use of plankton as food, there has existed a tendency to refer to plankton as if it were uniform in nature and abundance. Nothing could be further from the truth. The kind of organism which dominates the plankton differs markedly from place to place and from time to time (Sears and Clarke, '40). A pronounced change in the composition of the plankton may sometimes occur within a few miles or less, but on other occasions it may be uniform for large areas. At any one point the interval of time for a significant change in the plankton may be as short as a few days or as long as several weeks. Frequently the type and abundance of plankton at night differs from its complexion during the day as a result of diurnal migrations to and from the surface of the sea (Clarke, '34).

The animals which are usually most abundant in the zooplankton are the crustacea and particularly the copepods, although on occasion euphausids may predominate. In some situations medusae, salps, siphonophores, sagittae, or other soft-bodied animals may comprise more than 90 per cent of the zooplankton.

At certain seasons of the year and in certain localities, the phytoplankton may greatly outweigh the zooplankton. Species provided with long spines and those which grow in chains are often retained in coarse-mashed plankton nets intended for zooplankton. Under these circumstances diatoms may clog the pores of plankton nets to such an extent that the filtering efficiency is reduced nearly to zero.

The variability of the plankton is such that it would be exceedingly difficult to predict what type and what amount would be encountered in any given situation, at least until that area had been studied for a long time. The kinds of organism which will predominate in the plankton haul will depend upon which happen to be most abundant at the time, and to a certain extent upon the mesh of the net used. It is impossible to avoid catching undesirable species entirely.

The favorable conditions of slight sea, moderate wind, and rich plankton (1.0 cc. per m^3.) which existed for the present raft tests will not always be encountered. The abundance of the plankton in the open sea is ordinarily much less than that in coastal regions and values obtained in most tropical areas are regularly smaller than those of temperate or polar regions. An investigation extending over a period of a year and a half at stations in (1) the coastal water, (2) the "slope" water, and (3) the Sargasso water between Montauk Point, New York, and Bermuda revealed that the average volume of zooplankton in the slope water was only about one quarter as great as that in the coastal area, and the volume in the Sargasso water was only about one quarter as great as that in the slope water (Clarke, '40).

It is apparent that even in the richest coastal areas, plankton volumes as great as 1.0 cc. per cubic meter will not be encountered on every occasion and farther off shore such abundance will be found

less and less frequently. The amount of plankton taken by the raft during Test 2 should therefore be regarded as a maximum probable value rather than as a representative value.

Occurrence of poisonous species

Although only one species of plankton organism in the sea (*Gonyaulax catenella*) is known which produces a poison fatal to man, there are no doubt other forms which are more or less harmful. It has been suggested that the chitinous exoskeletons of the crustacea would be injurious in large quantities but this is probably not the case because of the ability of orientals to eat whole shrimps and grasshoppers. The sharp siliceous valves of diatoms have also been regarded as a danger, but these forms have long been eaten with impunity as part of the stomach contents of oysters, clams and other shellfish. It is not proposed to catch phytoplankton in large quantities, although this might be unavoidable in some situations. The recent outbreaks of the dinoflagellate, *Gymnodinium* sp. ("Red tide"), along the Florida coast have resulted in extensive fish mortality, but it is not known whether this organism is poisonous to terrestrial animals (F. G. W. Smith, 1947).

Dead and decomposing plankton is sometimes encountered in large quantities in the sea and fragments of dead fish, or of flotsam and jetsam, might be picked up undetected by the plankton net. Whether such material would be harmful to man is not known. In inland waters the decomposition of some of the blue-green algae is accompanied by the formation of hydroxylamine, a highly toxic substance for most domestic animals. Many deaths assigned to this cause have been reported from the middle western states where the animals had access to pond water in which blooms of blue-green algae were decomposing (Juday, private communication).

A more probable danger in the sea is the occurrence of stinging forms in the plankton. Certain jellyfish and other types of plankton are known to produce serious stings to the skin and these are sometimes followed by a general reaction of the whole body. Tentacles of the dangerous Portuguese Man-O-War, which may stream out for 30 feet or more, are often picked up by plankton nets. The results of swallowing any of these stinging forms might be still more serious than contact with the skin.

The planktonic flagellate, *Gonyaulax catenella,* is responsible for the poisonous quality of certain shellfish, particularly the mussel found on the coast of California and elsewhere (Sommer, Whedon, Kofoid, and Stohler, '37). The poison is accumulated in the digestive glands of the mussels, and has also been found in the digestive glands of such organisms as the sand crab, *Emerita.* It is also easily adsorbed on sand and the same, or a similar poison, has been obtained from mud on at least one occasion on the Atlantic Coast. The poison has been found to constitute approximately 6.5 per cent of the weight of *Gonyaulax* as a maximum. A variation in the poison content of 1 to 100 has been reported.

From the foregoing data and from the amounts of poison in mussels which are lethal, it may be calculated that a few million cells of *Gonyaulax catenella* could be fatal to man if ingested directly. The number of cells of this flagellate in sea water is subject to extreme variation, from none at all up to several million per liter. Blooms of 20 to 40 million cells per liter have been reported. When the concentration approaches one million cells per liter, this organism, like many others, causes the water to become rust red.

Gonyaulax catenella is described as a neritic, or coastal, species although it occurs in the "open ocean" rather than in enclosed bays and estuaries. This species has been reported from many points along the Pacific Coast, including the Gulf of California, Monterey, San Francisco, Washington, Canada and Alaska. *Gonyaulax catenella* has not been positively

identified from the Atlantic Ocean, although it has been "tentatively identified" from Nova Scotian and Belgian waters. It may appear also in other parts of the world where the plankton has not yet been thoroughly studied. Other species of *Gonyaulax* occur in both the Atlantic and the Pacific but there is no evidence that these species can produce the toxin.

Even with the use of relatively coarse zooplankton nets, quantities of the smaller plankton, such as *Gonyaulax,* will unavoidably be taken when such species are very abundant. In towing the No. 2 silk net for only one hour in Test 2 (table IV), 289 m^3. of sea water were theoretically filtered. As the pores of the net became clogged, the phytoplankton from far more than one liter would be retained in the catch, and we have seen that under some circumstances a liter of water could contain more than a lethal dose of *Gonyaulax catenella.* There would thus be definite danger of unwittingly catching a dangerous amount of this species in certain areas. *In addition, the possibility must be constantly kept in mind that other plankton forms, as yet unsuspected, may be as poisonous to man as is* Gonyaulax catenella.

Palatableness under starvation conditions

A major consideration in the provision of an emergency source of food is its palatableness under starvation conditions. If the material suggested for food is revolting because of its taste, smell, or appearance, it may cause nausea especially under conditions tending to produce seasickness. In such cases the food would lose whatever value for improving morale it might otherwise have.

Several tablespoonfuls of the drained plankton obtained in Tests 1, 2, and 3 were eaten by the individuals conducting the tests without ill effect. The plankton had a mildly pleasant taste, being somewhat reminiscent of shrimp or raw oysters. Six or eight other members of the ship's company who were definitely prejudiced against the idea at the outset, tasted the plankton and pronounced it either good or not objectionable. The plankton was also tasted after various treatments, such as being washed with fresh water, spread on bread or crackers with and without butter, or fried. Some subjects found that the plankton was most palatable in its original condition, but others preferred it after it had been treated with fresh water.

Larger quantities of the plankton obtained during the November collection were consumed by three of the investigators. No toxic effects developed after eating 100–200 grams (wet weight) of the material during the course of a day. The maximum quantity eaten by any one of the subjects at one time was 100 grams. Larger amounts were definitely unacceptable and distasteful. It is probable that psychological factors entered into the matter of the palatableness and digestibility of the plankton in the laboratory and at sea. Such factors are not easy to evaluate. It was certainly true that a quantity of only 30–40 grams of plankton gave the impression of remaining undigested in the stomach for several hours after eating.

Other types of plankton may be much less palatable than the samples consumed in the present case which were dominated by the shrimp-like copepods. The abundant presence of jelly-like organisms may produce a decidedly objectionable taste.

The reaction to a plankton diet of a starved individual adrift on a raft may be quite different. The experience of castaways has shown that, under the distress of starvation and thirst, the condition of the mouth and throat is such that certain types of materials cannot be swallowed, especially if there is no drinking water to accompany them. In the present investigation even small quantities proved to be nauseating if taken while collecting in a rough sea.

Nutritive value of plankton and effect on water balance

The composition of plankton in respect to potentially nutritive substances

will be expected to vary widely because of differences in the types of organisms present. The percentage of organic material on a volume or wet weight basis will be lower when jelly-like species are abundant and may differ considerably on a dry weight basis. A typical zooplankton catch (Sample C, table VII), consisting chiefly of copepods, yielded the following analysis when dried: fat 1–4 per cent, protein 52–59 per cent, carbohydrate 13–17 per cent, and total ash 19–33 per cent. The fat content of samples of copepod plankton was reported as 7 per cent by Johnstone ('08) and as 15–22 per cent by Vinogradov ('35 and '38), and may sometimes exceed 30 per cent. Vitamins and mineral salts useful from the nutritive standpoint are also present. However, it has been seen that rats could not assimilate the whole of these organic materials. Whether man or other terrestrial forms could do so remains to be determined. It is obvious that fish and other marine organisms which live largely, or entirely, on zooplankton are able to assimilate it satisfactorily. It would be desirable to ascertain the differences in the digestive processes of these forms and of rats.

To gain a rough idea of the maximum nutriment which might be obtained from eating plankton, we may assume that all the organic matter contained could be assimilated. On the basis of the foregoing analyses, and allowing 9 calories per gram for fat, and 4 calories for protein and carbohydrate, we may assign an approximate maximum energy content of 4 calories per gram dry weight for this type of plankton. Using the data of Sample A–3 (table VIII), in which the plankton was squeezed, 1000 cc. of plankton, yielding 82 grams of dried material, would provide 328 calories of energy. The 2400 cc. of plankton caught from the raft in Test 2, when calculated on a 24-hour basis, would have provided 788 calories if the whole amount could have been eaten and assimilated without harmful results (see below). This would represent about one-quarter of a man's average daily requirement under conditions of moderate activity (Clarke, '39). Considerably less energy might be required by life-raft occupants under some circumstances.

The facts thus far available indicate that it will never be possible to catch from a raft, consume and assimilate enough plankton to provide the entire energy of a maintenance diet. The amount of energy which can be obtained from this source will relieve the body of drawing upon its reserve supply of fat and other tissues to a corresponding extent. Survival without any food is possible for 30 days or more. During studies conducted by Dr. A. M. Butler, tests performed at the Harvard Fatigue Laboratory showed that an individual's physicial ability is not impaired after 6 to 8 days of very deficient intake of water and food. A partial diet may be of some physical benefit for longer periods and may possibly have morale value from the beginning. In regard to the use of plankton as an emergency food the essential question to be decided is whether a partial relief of the drain on the body's reserves is worth the difficulty and danger, if any, of catching and consuming plankton.

An approximate calculation may be made of the effect of a plankton diet on the water balance of the body on the basis of the chemical composition of squeezed plankton (Sample A–3) which represents the type of treatment most likely to be feasible on a life raft. Exact values cannot be obtained without actual trials with human subjects since the osmotic effect per gram of each solute found in the dry material is not known. However, an approximation of the water required for the renal excretion of a gram of plankton may be estimated as follows. Using the analytical data for Sample A–3, table VI, the milliosmols per gram are roughly:

	Mg.	Milliosmols
N	98.0	3.3 (as urea)
P	8.3	0.2
Na	44.0	1.9
Cl	82.0	2.3
		7.7 milliosmols

Allowing a small amount for other solutes, the total solute content may be considered as equivalent to 8 milliosmols per gram of dry weight. Since the maximal concentration of solutes in the urine which can be attained by the kidney is taken as 1.4 osmolar, the minimal volume to which the urine can be reduced without causing dehydration may be found by dividing the total solutes in the plankton by this value (Gamble and Butler, '44):

$$\frac{8.0}{1.4} = 5.7 \text{ cc.}$$

This means that about 5.7 cc. of water must be available to make possible the excretion of the metabolites resulting from the combustion in the body of each gram of plankton. Since the squeezed plankton contained 86 per cent water (table VIII), about 6 cc. of water would be taken in with each gram of dry material. In addition about one-third of a gram of metabolic water would be produced by the oxidation of each gram of plankton with a composition similar to that of Sample C (assuming values of 0.41 g. of water per g. for protein, 0.56 g. for carbohydrate, and 1.07 g. for fat). It is therefore possible that, in general, plankton may contain as much water as would be required for the excretion of all of its breakdown products. If this should be found true, any quantity of plankton could be eaten without disturbing the osmotic water balance of the body. Perhaps for this reason the whales which live on plankton diets may not require any modification in this respect of their mammalian type of kidney.

There is doubt that large amounts of plankton could be eaten by man for other reasons. When more than 500 cc. of sea water is drunk per day, diarrhea or vomiting may supervene and themselves cause dehydration (Butler and Gamble, personal communication). Since the salt content of squeezed plankton is about 70 per cent of that of an equal volume of sea water (table VIII), it might be impossible for a man to eat more than about 700 grams of wet plankton (i.e., the squeezed plankton from about 1200 cc. of drained plankton) per day without harmful results. The fact that the plankton is not in liquid form might allow these amounts to be increased somewhat.

The ratio of magnesium to potassium in sea water, and in the plankton analyzed in the present investigation (table IX), is much higher than in the body fluids of man. The consumption of large quantities of plankton, or its continued use, might therefore result in disturbing the salt balance of the body.

The possible effects of these differences in ionic ratios, and perhaps of others, are not known but must be considered. The high magnesium content of sea water may be the cause, in part, of the diarrhea produced in man by excessive intake of sea water. Unless the human consumer were informed of these possibilities, he might eat a harmful amount of plankton without realizing it. However, certain of the domestic animals might not be disturbed by these differences and, in contrast to the rat, might be found to thrive on a partial or a complete diet of plankton. Such a possibility should be examined in the future as it would enable man to make use indirectly of the tremendous potential food source represented by the plankton.

Summary

1. Observations are reported on the abundance and variability of the marine zooplankton, its chemical composition, its nutritional value when fed to rats, and its palatableness to man. In tests on the feasibility of the use of plankton as an emergency food, a maximum of 100 cc. of plankton, with dry weight of 5 to 11 g. according to treatment, was found to be obtainable per hour from a life raft.

2. The dry plankton was composed of 52–59 per cent protein, 1–4 per cent fat, 13–17 per cent carbohydrate and 19–33 per cent ash. The chloride content of the drained plankton was about 1.4 per cent of the wet weight, or about 80 per cent of that contained in an equal volume

of sea water, and was reduced to 0.25 per cent of the wet weight by washing and squeezing. The magnesium content, which was initially high, became relatively greater, following this treatment.

3. Estimation of the osmotic effect of the solutes present indicated that plankton may contain as much water as is required for the excretion of all its breakdown products when consumed by man. The high ratio of magnesium to potassium, however, might disturb the salt balance of the body.

4. Rats fed on plankton lost weight rapidly and died within 4 to 19 days but survived about 30 per cent longer than starved rats. Rats fed on a diet composed of ⅔ meal and ⅓ plankton, and of ⅓ meal and ⅔ plankton, failed to grow as fast as rats on a full diet of meal but fared better than those on the fractional diet of meal only. The rats therefore derived some nourishment from the plankton but were able to assimilate only a small fraction of the food energy which it contained.

5. Plankton with the observed chemical composition was calculated to have an approximate maximum energy content of 4 cal./g. dry weight. The 2400 cc. of plankton which could theoretically be obtained from a life raft in 24 hours would thus provide 788 calories, if it could all be assimilated, or about ¼ of a man's average daily requirements. The advantages, difficulties, and possible dangers because of poisonous species, of the direct and indirect use of plankton by man are discussed.

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Contribution No. 426

OCEAN BOTTOM SAMPLER FOR SHIPS UNDER WAY

BY

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Reprinted for private circulation from
GEOPHYSICS
Vol. 13, No. 3, July, 1948

OCEAN BOTTOM SAMPLER FOR SHIPS UNDER WAY*

J. L. WORZEL†

ABSTRACT

A simple bottom sampler has been developed which may be used from ships under way at speeds up to 12 knots. The sampler is allowed to fall freely under its own weight, and is recovered by reeling in a wire attached to the front. An open tube at the front will obtain about ½ pint of surface material from mud, sand, gravel, or coral bottoms. Existing models have been used in depths to 300 fathoms. At a speed of 8 knots, using a winch with a ¾-h-p. motor, one man can take a sample in 3 minutes in 10 fathoms of water, and in 8 minutes in 100 fathoms.

Models have been built with trap doors to close the tube after taking the sample, and to allow the water in the tube to escape when the sample is taken. These have been discarded as the improvement in the samples was negligible. The sampler can be easily combined with free-falling hydrographic instruments, such as the bathythermograph.

Operation under way improves the ease and accuracy with which the position of a sample may be fixed as the ship can maintain its speed and course. It greatly increases the area covered and the number of samples taken in a given time.

INTRODUCTION

Bottom samples have been used for many years as aids to navigation, and in marine biological investigations. During the past 30 years, the increasing use of sonic and supersonic instruments for sounding and echo ranging has created a demand for bottom-sediment charts to correlate observed variations with bottom materials. More recently, geochemical and sedimentation studies have created a further demand for samples of the ocean floor.

The oldest and simplest equipment for bottom sampling is the sounding lead armed with tallow or grease. This can be used under way at slow speeds, but has many obvious disadvantages. To obtain better bottom samples, dredges and coring tubes have been used.[1] (Reference 1 has a good survey of all types.) These devices require that the ship be stopped, which slows down the work and greatly reduces the precision with which locations may be fixed. The sampler described here can be used while the ship is under way, and will obtain samples of mud, sand, gravel, or coral bottoms, satisfactory for most investigations.

CONSTRUCTION OF SAMPLER

The bottom sampler (Fig. 1) consists of a sample tube, a body weight, a body extension member, and tail fins. The sample tube is made of brass or steel tubing,

* Contribution No. 426 of the Woods Hole Oceanographic Institution. This work was carried out under Contract NObs 2083 of the Bureau of Ships, Navy Department.

Presented at the Annual Meeting of the Society, Los Angeles, California, March, 1947. Manuscript received by the Editor, January 13, 1948.

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[1] Jack Hough, "Bottom Sampling Apparatus," *Recent Marine Sediments, A Symposium* (Tulsa, Oklahoma: A.A.P.G., 1939), pp. 631–664.

round or square, about 10 inches long, and 2 inches in diameter. The free length inside the tubing of these dimensions must be greater than 6 inches in order to retain the sample; but lengths greater than 8 inches show no improvement in the size of the sample or the ability to retain it. The sample tube forms the nose of the instrument. About 2 inches of the tube overlap on the body weight and are fastened to it with a simple screw or bayonet connection for convenience in cleaning.

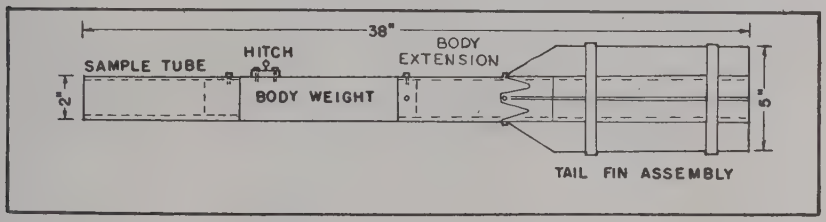

FIG. 1. Underway bottom sampler.

The body weight is a bar of brass or steel, 12 to 15 inches long, with a suitable eye for a cable attachment just behind the sampler tube. The body extension member is made of tubing similar to the sample tube, about 10 inches long, and is attached to the rear end of the body weight. Four tail fins, each with an area of 16 to 20 square inches, are attached in a cross shape at the rear of the body-extension member.

With this arrangement of parts, the sample tube strikes bottom first when the instrument falls freely; but is uppermost while the sampler is being recovered.

The first samplers were built with a shear pin at the forward cable attachment, and a permanent attachment at the tail to facilitate recovery of the sampler if fouled on the bottom. This precaution proved unnecessary and has been abandoned.

OPERATION

Free-fall method.—The operation of the sampler (Fig. 2) is an adaptation of a method first successfully used by Ewing and Vine in 1940 for bathythermograph observations from ships under way. The sampler is allowed to fall freely in the water, and the wire is paid out as required by the fall of the sampler and the movement of the ship. When the sampler strikes bottom, the wire becomes slack. The winch brake is then applied and the sampler quickly rises to its equilibrium level close to the surface, which is determined by the speed of the ship, the amount of wire paid out, and the weight and drag coefficients of the wire and sampler. The strain on the wire from the sudden application of the brake is not excessive, due to the shock-absorbing action of the large curve of the wire. Shortly after the main strain has passed, the winch clutch is engaged and the instrument recovered.

The principal force to be overcome in recovering the instrument is the drag of the wire, so it is desirable to use the smallest wire possible. For instruments weighing 25 pounds or less, and wire lengths up to 2,000 feet, 1/16-inch 7×7 -strand stainless steel airplane control cord, with a breaking strength of 900 pounds, is used.

Electric winch.—A small electric winch is used, with a ¾-h-p. motor for intermittent, and a 1½-h-p. motor for continuous operation. These are stock

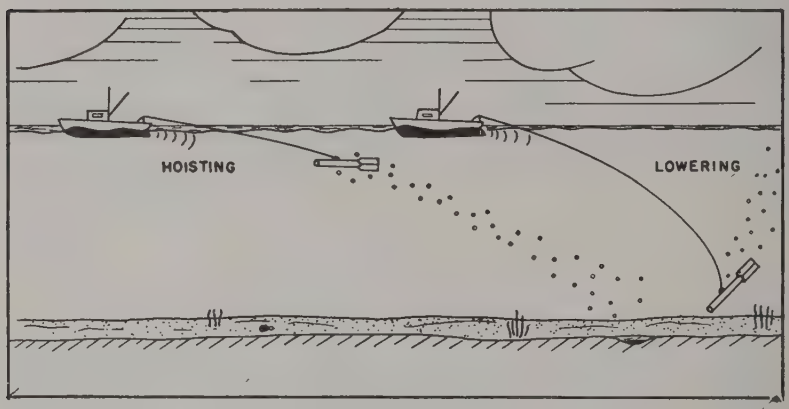

FIG. 2. Method of taking bottom sample.

1,600 r.p.m. motors, geared down, using one countershaft, by a 12-to-1 ratio, so that the winch drum turns at 133 r.p.m. The drum is brass, base diameter 10 inches, width 4 inches, and flange width 2 inches. Brake and clutch are on the same lever, the brake at one extreme, the clutch at the other; on center the clutch is disengaged and only the drum shaft turns as the cable pays out. A counter is attached to the drum shaft to determine the amount of cable paid out at any time.

MODIFICATIONS

Trap-door models.—A sampler has been made with a trap door over the end of the tube to prevent washing of the sample. The door is closed on contact of a trigger with bottom (Fig. 3, Type A). Qualitative comparisons of samples taken in the same area with open-ended and trap-door models show no discernible difference. No quantitative comparisons have been made.

Another model has two trap doors (Fig. 3, Type B), one in the nose and one at an opening in the back end of the sample tube, to allow the water in the tube to escape freely when the sample is taken. No appreciable gain in sample size is observed.

Trap-door models have an advantage in rough weather. If the boat rolls as the instrument is brought out of the water, the tail fins may contact the water

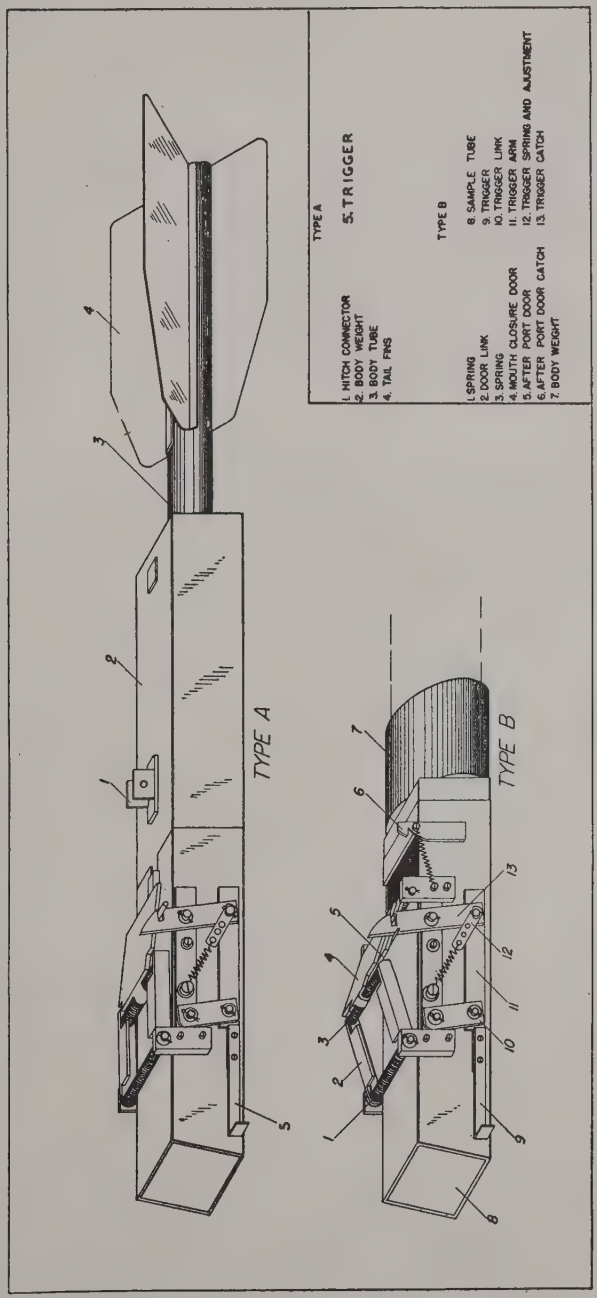

FIG. 3. Design details of two types of bottom samplers.

again, and the sampler may flip over. An open-mouthed model will then usually lose the sample, while a trap-door model will retain it. This loss can, however, largely be avoided by skillful operation of the winch. The advantages of trap-door models are not sufficient to justify their complicated construction, and the open-ended sampler has been adopted as the standard model.

Combination with hydrographic instruments.—Hydrographic instruments operating on the free-fall principle can easily be adapted to take bottom samples, provided their operation is not impaired by the jar of contact with bottom. For example, the bathythermograph, developed by Ewing and Vine, which gives a continuous record of temperature versus depth, was made to take bottom samples by the addition of an open tube on the nose. No damage to the temperature or depth-recording mechanism has been observed. Samplers have also been built with a depth-recording gauge in the body tube which automatically gives the depth at which a sample is taken.

CONCLUSIONS

The samplers described above have been used in water depths to 300 fathoms. Heavier instruments can be designed, and operation in depths of the order of 1,500 fathoms is reasonable. Samples of mud, sand, gravel, and coral have been taken, varying in size from about two pints for soft mud to a tablespoon for coarse gravel; the average size is about $\frac{1}{2}$ pint. Fresh chips of rock have also been recovered.

The only losses of instruments to date were caused by the ship's propellor cutting the wire as a result of poor communication between observer and ship's officers, not of the ordinary yawing of the ship. No samplers have yet been lost by fouling on bottom.

Samples can be taken at speeds from 0 to 12 knots. At a speed of 8 knots, one man can take samples at 3-minute intervals in 10 fathoms of water, and at 8-minute intervals in 100 fathoms. The position of a sample can be located as accurately as the navigation of the vessel permits. Rapid reconnaissance or closely spaced surveys may be made. A recent survey was made with the sampler in one-fifth the time necessary for similar work with dredges, snappers, and coring devices.

ACKNOWLEDGMENTS

Thanks are due to Maurice Ewing and A. C. Vine for their advice and assistance.

Contribution No. 427

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Reprinted from Proceedings of the Society for Experimental Biology and Medicine,
1948, **67**, 440-445

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Factors Influencing the Growth of Integumentary Pigment in Fishes. I. The Role of Light.*†

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It is a common observation that light is associated with changes in body pigmentation such as "tanning." Numerous clinical observations[1-5] indicate that certain types of pigmentation deficiencies in man may be corrected by light treatment. In lower mammals Bissonnette and others have demonstrated that pigmentation may be influenced by illumination while experimental evidence has accumulated indicating the importance of light in producing integumentary pigmentation in lower vertebrates. Cunningham[6-8] working with flatfishes; Herbst and Ascher[9] using salamander larvae; Vilter[10] studying axolotls; Sumner and Wells;[11] Sumner and Doudoroff;[12] Odiorne;[13] Sumner;[14-16] Os-

* This work was aided in part by a Bache Fund grant administered by Professor G. H. Parker and in part by equipment provided by the Elizabeth Thompson Science Fund.

† Contribution No. 427 of the Woods Hole Oceanographic Institution whose research facilities were generously provided for this investigation.

‡ Now located at Syracuse University.

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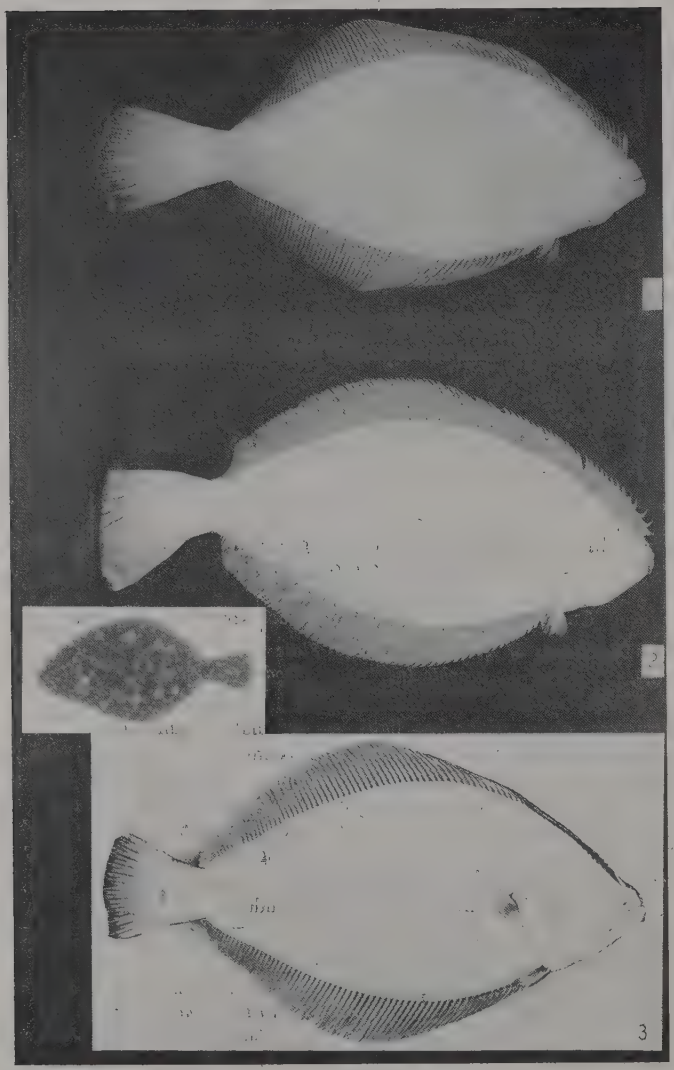

PLATE I.

All figures shown are photographs of the lower surface of living summer flounders. Each animal is selected as typical for the particular experimental situation.

FIG. 1. Normal control freshly caught. The entire ventral surface is free from melanophores.

FIG. 2. Fish black-adapted 2 days, blinded and maintained in darkness 30 days. Entire surface is white as in the control fish except for a few pigmented regenerated scales.

FIG. 3. Animal black-adapted 3 days, blinded and kept for 41 days in a black tank brightly lighted from above. About 2.0 Weston units of light. Somewhat more pigment has developed here than in either of the above figures.

born;[17-21] and Dawes[22] experimenting with various species of fishes have all reported experiments concerning integumentary pigmentation in which light was an important factor. In recent work[17-21] it was found that melanophore development in normally non-melaninated areas depended upon the maintenance of two general conditions. First, the internal environment must be one which favors darkening in the normally pigmented areas; and, second, the external environment must provide illumination (direct or by reflection) to the integument.

The experiments reported here were designed to obtain more detailed information on the role of light in the development of melanophores on the normally unpigmented surface of the summer flounder.

Materials and Methods. Summer flounders freshly caught from Woods Hole waters were used for the experiments. The water temperature for all experiments ranged between 18 and 21°C. The experimental fishes were background-adapted in black tanks illuminated artificially from above. Light intensity (reflected or transmitted) was measured by a Weston exposure meter. The following modifications were made on the ventral illumination tubs previously described:[17] (a) removable false bottoms of perforated glass were rested upon glass supports ¾ inches above the permanent glass floor to allow water to circulate between the 2 glass plates and protect the lower surface of the fishes from overheating; (b) three independent water inlets near the bottom of the tub provided rapid circulation and adequate overflows connected to variable level standpipes allowed easy adjustment of the water level; (c) the light intensity was increased by using a total of 600 Watts for each glass bottomed tub and the walls and ceiling of these special tubs were white to produce a high incidence of internal reflection.

After being black-adapted, the experimental flounders, 106 in all, were totally blinded by enucleation. Opaque masks of black cloth were held in position by suturing each corner to the base of an adjacent fin ray. This kept the mask securely in place without hampering the normal movements of the fishes. Photographic records of the living fishes were made at frequent intervals, supplemented by others of preserved animals.

Adequate unoperated control animals (Fig. 1) in a natural environment were available for purposes of comparison as the experiments progressed.

Experimental. Summer flounders previously black-adapted and totally blinded were placed in total darkness (Exp. 1); subjected to different amounts of overhead illumination where mostly *reflected* light reached the ventral surface (Exp. 2, 3 and 4); exposed to *direct* intense illumination ventrally without masking local areas (Exp. 5) or protecting parts of the ventral surface with opaque masks (Exp. 6).

Exp. 1. Summer flounders black-adapted then blinded as previously described were kept in total darkness from 2 to 6 weeks. Without exception these animals failed to develop any general melanination on the ventral surface (Fig. 2). Here and there a black scale did appear but all were cases of regenerating scales where the original had been lost during experimental manipulation. This will be considered as a constant in subsequent experiments described here. The pigmentation of regenerated scales comprises a special situation which must not confuse the objectives of these experiments.

Exp. 2, 3, 4. These 3 experiments embraced changes in intensity of light source and shade of background so that the light reflected from the surfaces was 0.1 to 0.2, 2.0, and 16.0 Weston Units respectively. Considering the findings from these experiments collectively it was observed that the most ventral melanin appeared on those fishes illuminated most intensely and long-

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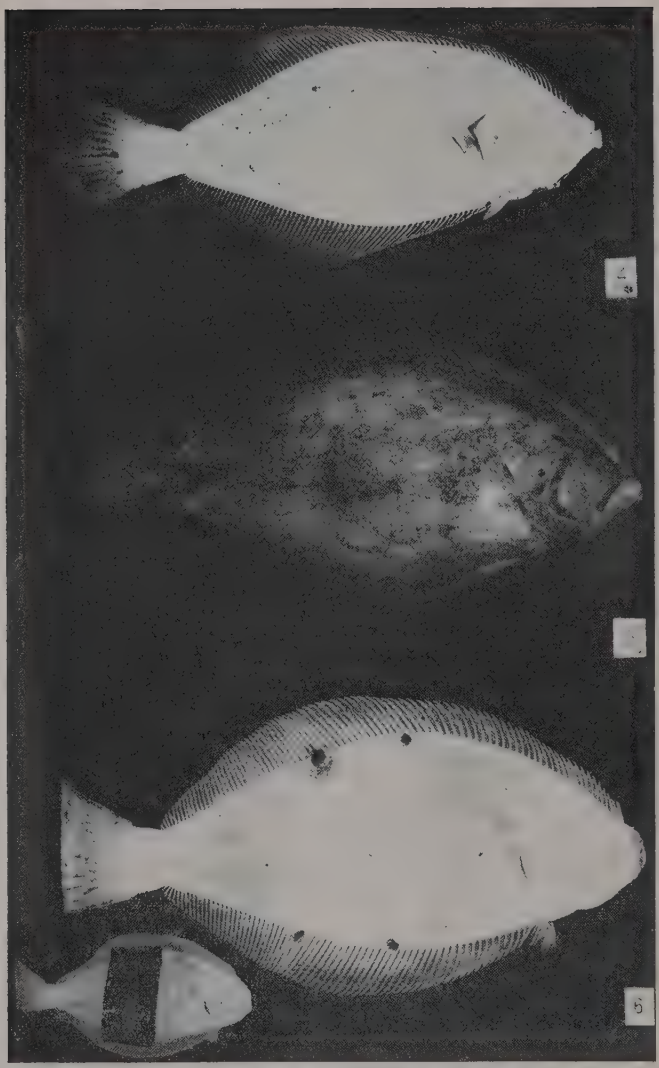

PLATE II.

All photographs are of the normally unpigmented ventral surface of living summer flounders. All inserts are further reductions of the corresponding animal.

FIG. 4. Summer flounder black-adapted 2½ days, blinded and placed in a brightly illuminated white tank (reflecting about 16 Weston units) for 28 days. A considerable increase in ventral melanophore production over that seen in the previous figures.

FIG. 5. Black-adapted 2 days, blinded and maintained in the special apparatus providing direct ventral illumination of high intensity (about 400 Weston units) for 26 days. First evidence of melanin formation was noted at about 90 hours. Note that the ventral surface has become quite completely darkened by an extensive covering of melanophores.

FIG. 6. This fish was maintained under the same conditions as described for Fig. 5. In addition an opaque mask was affixed to cover part of the ventral surface (see insert). This mask was kept in place during the entire sojourn of the animal in the ventral illumination apparatus (26 days). The mask was removed and the photograph taken at the end of that time. The area protected from the light is free from melanophores.

est. Fig. 3 and 4 illustrate typical cases.

Exp. 5. In this experiment intense light (400 Weston Units or 25X as much as was used in Exp. 4) was directed to the ventral surfaces of the fishes through glass bottomed tanks. This method provides two significant advantages. First, it is possible by using various lamps to subject the lower surface of the experimental animal to any intensity desired; and second, it is possible to measure with accuracy the amount of light falling directly upon the lower surface of the fish. Thus, illumination may be rigidly controlled.

Under such favorable conditions pigment formation proceeded rapidly. Frequently it was possible to detect some evidence of melanophore formation during the fourth day of illumination and after 4 weeks of such treatment the entire ventral surface was found to be generally darkened with an extensive growth of melanophores (Fig. 5).

Exp. 6. Success in blackening the ventral surface so completely with melanophores in a relatively short time suggested an experiment designed to determine whether the pigmentation response was due to the *direct* effect of illumination, assuming the internal environment to be optimum in all the experiments, or whether it was necessary only that light *be present* for the reaction to continue. It was reasoned, therefore, that if it were necessary for light to fall directly upon the cell (direct effect) areas covered by an opaque mask would remain unpigmented while exposed areas would develop melanophores as in Exp. 5. On the other hand if it was necessary only that a fish with optimum *internal* physiological conditions be generally illuminated one might expect that the pigmentation reaction would go on underneath the mask regardless.

Accordingly, flounders prepared as in Exp. 5 were further provided with opaque masks as described previously (Fig. 6—insert). They were illuminated ventrally (400 Weston Units) as before and simple, clean-cut results were obtained. The exposed surfaces became melaninated but the protected area remained as free from pigmentation as in the control fishes. This striking result seen in Fig. 6 seems to indicate clearly that light provides a direct stimulus to the particular cell destined to develop into a melanophore by producing melanin.

Discussion. It becomes clear from the data presented that light is not only a very significant factor in the experimental development of melanophores in a normally unpigmented area but also that there is a correlation between the amount of pigment grown, the intensity of the light and duration of the exposure. Data of a sufficiently quantitative nature to determine whether this relationship is direct over all ranges of light intensity are not available. It is probable, however, that a direct relationship between light intensity per unit time and degree of melanination would not hold in ranges of very high intensity. The physiological limit of the rate at which melanin could be formed would probably be reached before arriving at extremely high intensities of light.

The impression should not be gained from these experiments, however, that light is the most important single factor in the production of melanophores. Although it is obviously an essential factor (except perhaps in the case of regenerated scales) it must be emphasized that the condition inside the cell as evidenced by the degree of dispersion of melanin granules in the cells of normally pigmented areas must represent the darkening phase of the fish. The ineffectiveness of high intensities of light directed on the surface of a flounder while in a physiological condition not favoring darkening is strikingly shown in the case of a white-adapted fish where, instead of melanin production one witnesses an actual decrease in dark pigmentation due to melanophore degeneration.[12,13,22] The observation that in physiologically dark flounders regenerating scales develop melanophores even in the absence of illumination is further evidence that in certain instances light is not necessary for the growth of melanin in melanophores. The problem of the pigmentation of regenerating scales represents a special case which deserves more detailed investigation in the future.

Summary. 1. In addition to a favorable internal environment in the cell, light is necessary for the development of melanin in

melanophores of intact scales.

2. Light passing directly through glass bottomed tanks onto the lower surface of the flounders was the most effective in producing melanophores. This means of illumination delivered the most intense light to the ventral surface of the fish and could be most accurately measured.

3. The use of opaque masks indicates that light affects the cell directly to produce melanin.

4. The melanination of regenerating scales is apparently not dependent upon the presence of light. Investigation of this special problem is being continued.

Contribution No. 428

Preprinted from
TRANSACTIONS of the American
Institute of Electrical Engineers
33 West 39th St., New York, N. Y.

Printed in the United States of America
11/4/'48 Volume 67, 1948

An Instrument for Recording Continuously the Salinity, Temperature, and Depth of Sea Water

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MEMBER AIEE

MANY physical phenomena in oceanography can be determined from knowledge of the horizontal and vertical distributions of the salinity and temperature of sea water. Current practice in obtaining salinity measurements makes use of sampling devices and chemical analyses.[1,2] Surface temperatures are measured with conventional-type thermometers and thermographs. Measurements at subsurface levels are made with reversing thermometers[1] and with mechanical "bathythermographs,"[3] which provide a record of temperature as a function of depth. Although these methods provide highly accurate information, the lack of continuity of salinity data may at times limit their usefulness. Also, considerable time is consumed in the procedures of sampling, analysis, and plotting of data, and it is often difficult to retain navigation.

The instrument described measures continuously the temperature and specific electrical conductance of sea water, and computes from these its salinity. The measured temperature, the computed salinity, and the depth at which the measurements are being made are recorded simultaneously on a strip chart.

The instrument operates from a 115-volt 60-cycle supply and is unaffected by normal voltage and frequency variations or by the vibration and motion of the vessel. It measures the temperature of the water over a range from 28 to 90 degrees Fahrenheit with an error not greater than 0.2 degree Fahrenheit. Salinity is determined over a range from 20 to 40 parts per thousand ($^0/_{00}$) with an error not greater than $0.3^0/_{00}$. The maximum error in depth over the range from 0 to 1,200 feet is 12 feet. The time lag of the instrument is governed primarily by the thermal speed of response of the resistance thermometer bulb, which has a time constant of 0.45 second.

Although the precision is less than that obtainable by standard reversing thermometers and titrations for chlorinity, this disadvantage is offset for many purposes by the convenience of continuous measurement, and the prompt availability of the temperature and salinity data.

Several earlier instruments for determining the salinity of sea water from conductivity measurements are described in the literature.[4–9] These instruments employed Wheatstone bridge circuits by which the conductivity of a batch or flowing sample of sea water was compared with that of a standard of known salinity contained in a sealed cell while both were maintained at the same temperature. While this method provided a high degree of accuracy, the use of a sealed cell for temperature compensation introduced a serious time lag, and limited the practical application of these equipments.

Paper 48-173, recommended by the AIEE instruments and measurements committee and approved by the AIEE technical program committee for presentation at the AIEE North Eastern District meeting, New Haven, Conn., April 28–30, 1948. Manuscript submitted February 9, 1948; made available for printing March 3, 1948.

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Contribution Number 428 from the Woods Hole Oceanographic Institution.

Material for this paper is based on studies and results of a joint research and development project by the Woods Hole Oceanographic Institution and The Bristol Company under the sponsorship of the Navy Department's Bureau of Ships.

The author wishes to acknowledge the contributions of Dr. Alfred C. Redfield, Allyn C. Vine, and Dr. William A. Ford and John F. Holmes, all of the Woods Hole Oceanographic Institution, who, respectively, directed the project, initiated the development, and conducted the field tests; and John L. Russell of The Bristol Company, who was responsible for the mechanical design.

General Description

The instrument consists of three major units; the measuring elements assembly, the computing and recording mechanisms, and the amplifier unit. The electrical connections between the units are made with multiple-conductor cables and plug-type connectors, so that no tools are necessary in hooking up the equipments. Figure 1 shows the instrument installed in the Woods Hole Oceanographic Institution research vessel Balanus.

The measuring elements assembly, shown partly in section in Figure 2, includes a resistance thermometer bulb, a conductivity cell, and a Bourdon pressure element. The resistance bulb has a thermal time constant of 0.45 second and is capable of withstanding external pressures in excess of 2,000 pounds per square inch. It is constructed by drawing a number of strands of enamelled nickel wire into a long, small-diameter, thin-walled copper capillary tube, sealing the ends, and winding the tube on an open frame to form a helix. The connections are brought out through one end with kovar-glass sealed terminals. The conductivity cell is made up of a plastic tube sheathed in heavy bronze tubing and includes three coaxial platinum-lined electrodes, one in the center and one at each end. The Bourdon depth element is made of a beryllium copper alloy. Its free end carries a contact which moves across a slide-wire, converting a position measurement to an electrical value which can be easily transmitted. A single 9-conductor waterproof cable connects the measuring elements assembly to the recorder. The several sections comprising the housings for the measuring elements are bolted together, using confined rubber gaskets to make the complete unit pressure tight.

The computing and recording mechanisms are mounted on a steel frame enclosed in a wood case having removable sides and top cover. The top view of this

unit is shown in Figure 3. The measuring and computing mechanisms are electromechanical servo systems. The chart drive mechanism is provided with a speed change lever which can be used to change the chart feed rate from a given number of inches per hour to the same number of inches per minute. In addition, several sets of change gears are provided to permit many different chart speeds to be obtained. The maximum speed is 12 inches per minute. The three recording pens deflect about a common axis, and each uses a characteristic color of ink for making its record. A fourth pen, fixed in position, indicates any lateral departure of the chart, making it possible to correct the readings should a departure occur. The chart has 62 uniform divisions and has printed on it three sets of scales, one for each of the required measurements. One division on the chart corresponds to the following increments; 1 degree Fahrenheit in temperature, 0.2‰ in salinity, and 20, or 10, feet in depth, depending upon the calibration of the depth measuring element. Two salinity ranges are provided; 20 to 32‰ and 28 to 40‰, a switch being used for setting the desired range. The specific conductance of the sea water is indicated by a dial visible through a window in the front of the case.

Four identical amplifiers, housed in a single open-type case, are used to increase the power available from the measuring and computing circuits to a level sufficient for operating the various balancing motors. All of the electrical connections to each amplifier are made with a single plug-type multiple connector.

The mechanical construction of the instrument is sturdy, and it will not be damaged by reasonably rough handling. Where fixed mechanical relationships must be maintained for accurate performance, the units involved are pinned together or to supporting structural members with close-fitting dowels. All metal parts are protected from corrosion by Navy-approved methods for shipboard equipments.

In order to prevent ambient temperature errors all fixed resistors and slidewires in the measuring and computing circuits are wound with resistance wire having a negligible temperature coefficient. To insure long satisfactory performance, all capacitors and transformers used in the instrument are sealed hermetically.

Discussion of Design

Temperature System

The selection of a resistance thermometer for the temperature measuring element was made after considerations were given to various types of systems. These included the resistance thermometer, liquid-filled and vapor-tension type bulbs, and thermocouples. The systems were compared for accuracy, reproducibility, speed of response, scale distribution, and measuring and servo system requirements. The resistance thermometer arrangement was selected because it appeared to offer the best compromise among these factors.

Resistance thermometer bulbs can be reproduced with an accuracy of 0.1 degree Fahrenheit or better, and by suitable design the time constant can be made small, in the order of one-half second. The scale distribution, which depends upon the type of temperature-sensitive wire and the circuit used, can be made nearly linear. A simple Wheatstone bridge circuit energized from an a-c source can be used to measure the resistance of the thermometer bulb.

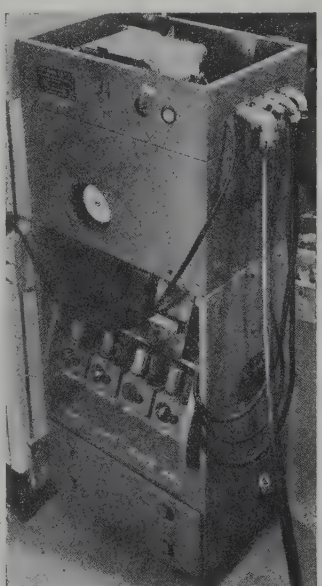


Figure 1. Shipboard installation of salinity-temperature-depth recorder

Variations in the supply voltage affect only the sensitivity of measurement. A simple a-c electronic amplifier can be employed to provide the necessary output power, and the performance of the system can be made so that large variations in the contact resistance are negligible.

Conductivity System

Laboratory measurements of the electrical conductivity of a solution are usually made with a 2-electrode cell and a Wheatstone bridge circuit. When this type of cell is immersed in a solution the measured conductance includes the conductances of the paths within and external to the cell. Since the cross-sectional area of the external shunt path may be very large for a cell submerged in the sea, its conductance will be large compared to the conductance within the cell. A cell with an electrode at each end may be effectively short-circuited when used in this way.

To avoid this difficulty a cylindrical cell with three coaxial electrodes is used. One electrode is in the center of the cell and one at each end. The two outer electrodes are connected together electrically, and the potential is applied between them and the center electrode. The lead to the center electrode is insulated, and approximately half of the current in this lead flows through the sea water sample to each end electrode. The two paths from the center electrode being in parallel, the measured conductance is the sum of the conductances of these paths. As the two outer electrodes are short-circuited together, they are at the same potential and no current will flow between them through any external shunt path. Thus, the measurements are independent of external shunt conductances and the cell constant may be determined without the need for duplicating the actual conditions of use. Moreover, this permits the use of a heavy protective metal sheath around the cylindrical cell, eliminating the possibility of shock damage to the plastic tubes which comprise the cell body.

A Wheatstone bridge circuit can be used to measure the conductance of the sea water in the cell, the bridge being energized from an a-c source.

Depth System

The depth of a measuring element can be determined best by measuring the sea pressure at that depth. Pressure is related to depth by considering the average specific gravity of the sea water to be 1.025. Although the actual specific gravity may differ from this value because of temperature and salinity conditions, the integrated error is usually negligible.

Pressure is most simply measured with calibrated spring elements, such as Bourdon tubes or bellows arrangements. The choice between these is governed by the factors; required power output, permanence of calibration, freedom from hys-

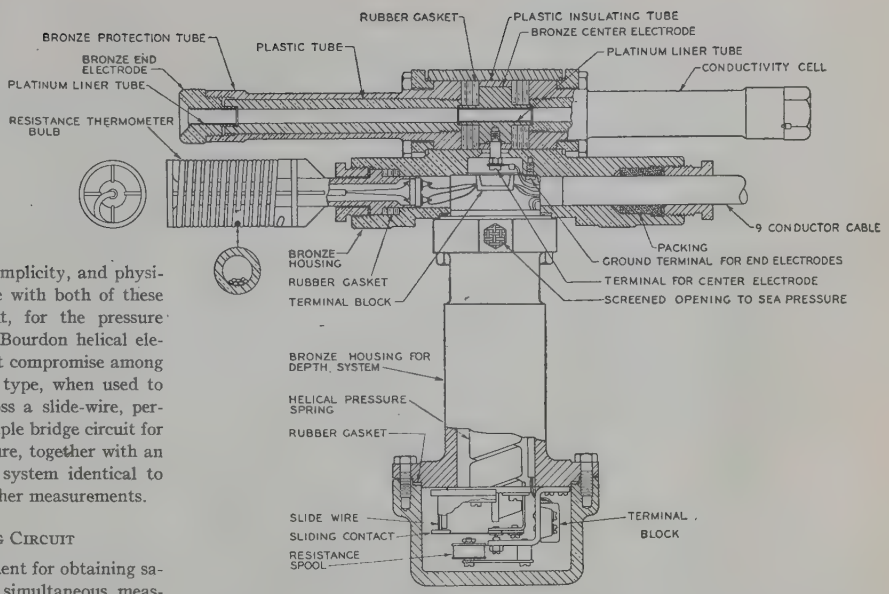


Figure 2. Section view, measuring elements assembly

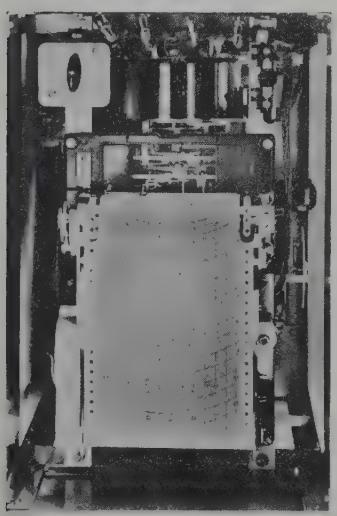
teresis, mechanical simplicity, and physical size. Experience with both of these types indicated that, for the pressure range involved, the Bourdon helical element offered the best compromise among these factors. This type, when used to move a contact across a slide-wire, permits the use of a simple bridge circuit for measuring the pressure, together with an amplifier and servo system identical to those used for the other measurements.

Salinity Computing Circuit

A circuit arrangement for obtaining salinity directly from simultaneous measurements of temperature and conductivity was preferred to the use of a temperature compensating cell as employed in previous instruments.[4,5,6,9] The slow response of a sealed cell designed to withstand the necessary pressure makes it less useful in a hydrographic instrument.

The use of a sealed reference cell in a bridge circuit for determining salinity does not provide exact compensation even when the sample water and the water in the sealed cell are maintained at the same temperature. An examination of the errors shows them to be only slightly less than those for the computing arrangement employed in the present instrument. However, serious errors may result from the difference in temperatures of the water in the measuring and reference cells caused by the thermal lag of the reference cell. Since it was expected that a resistance thermometer bulb could be made with less thermal lag than a sealed cell designed for the same pressure, thus permitting the high-speed performance desired, the computing method was selected.

Figure 3. Recorder, top view



The mathematical functions employed for the computation of salinity were derived from published data[10] relating conductivity to chlorinity and temperature. These data were translated to provide salinity as a function of conductivity and temperature by the use of the relationship

$$\text{Salinity} = 1.805 \times \text{Chlorinity} \qquad (1)$$

in which chlorinity is defined as the total amount of chlorine, bromine, and iodine in grams contained in one kilogram of sea water, assuming that the bromine and iodine had been replaced by chlorine. This expression differs by $0.03^0/_{00}$ from the empirical equation

$$\text{Salinity} = 0.03 + 1.805 \times \text{Chlorinity} \qquad (2)$$

which was established by an International Commission[11] based on samples collected from the Baltic Sea. Since the maximum possible error arising from the use of equation 1 instead of equation 2 amounts to only $0.03^0/_{00}$ and is less than the expected error of the instrument, the employment of the simpler relation is justified. Figure 4 shows the relationships between the specific conductance of sea water and the salinity for the temperature range 30 to 90 degrees Fahrenheit.

When these data are plotted with temperature as the parameter, all of the curves of the family obtained diverge from the origin, and each is slightly concave toward the salinity axis. When the logarithms of salinity are plotted against the logarithms of conductivity for each temperature value, all of the curves are approximately parallel and very nearly straight lines. If they were exactly straight and parallel, it would be possible to represent salinity precisely by the product of two independent functions; one of temperature, and the other of conductivity. By adjusting these curves so that this condition exists, an approximate function of this form is obtained. This complete family of adjusted curves can be represented with reasonable accuracy by the empirical equation

$$S = \left(\frac{100{,}000}{25.661 + 0.73720T} - 348.87\right)c^{1.0948} \qquad (3)$$

where S is the salinity in parts per thousand, T the temperature in degrees Fahrenheit, and c is the specific conductance in mhos per centimeter cube. This particular approximation was selected to give the error distribution indicated in Figure 5. It will be noted that the least errors are incurred for salinities between 30 and $35^0/_{00}$. The average salinity of the surface waters of the oceans is about $35^0/_{00}$. In

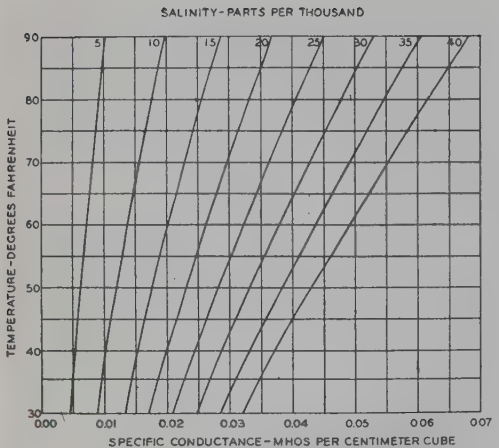


Figure 4. Salinity of sea water from temperature and specific conductance

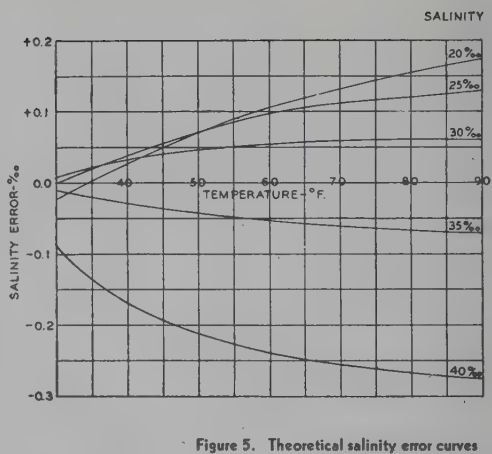


Figure 5. Theoretical salinity error curves

coastal waters it is approximately 32‰. Only in some of the enclosed seas in geographical areas where the evaporation exceeds the precipitation, such as the Mediterranean and Red Seas, does the salinity approach 40‰. Salinities less than 30‰ are encountered in coastal areas near river mouths and in some enclosed seas, as the Black Sea and the Baltic.

In order to perform the computation indicated by equation 3, mechanisms are required for deriving the necessary functions from independent measurements of temperature and conductivity, for multiplying these functions, and for indicating the product by the position of a pen on a chart. Although a much simpler mechanism can be employed for obtaining salinity when a sealed reference cell is used, the computing system was selected as the most practical arrangement chiefly because it makes rapid continuous measurements possible by reducing the time lag to that of the thermometer bulb.

Discussion of Circuits

Amplifiers and Servomotors

In order to provide the power necessary to operate the computing and recording mechanisms the output of each bridge circuit must be amplified. All of the measuring and computing circuits are energized with alternating current of line frequency. The output from each bridge is supplied to an independent electronic amplifier which operates the balancing servomotor of the bridge.

Each amplifier includes a rectifier tube, three stages of resistance-coupled voltage amplification, and a power stage. The tubes are operated below normal ratings to increase their useful life, and ordinary variations in their characteristics have no effect on the performance of the systems. The input resistance of each amplifier is approximately one-quarter megohm, and as the measuring and computing circuits are used in a null-balance manner, large changes in the resistances of the sliding contacts have only small effects on the sensitivities of the measurements. By incorporating a gain control in each amplifier the same type of amplifier serves for both the measuring and computing circuits.

The servomotor employed with each circuit is a small 2-phase induction motor, one phase being energized from the line and the other from the amplifier output. Its direction of rotation depends upon the relative phase of the amplifier output voltage with respect to the line and its speed is a function of the magnitude of this voltage. The slide-wire contacts and their associated recording pens are geared to their respective motor shafts, so that a direct relationship exists between them. The time for full-scale deflection of each of the measured and recorded quantities is approximately five seconds.

Temperature Circuit

Figure 6 is a diagram of the Wheatstone bridge circuit used for the temperature measurement, in which *R6* represents the thermometer bulb, connected to the circuit by three leads, *R1* is a slide-wire, and *R2*, *R3*, *R4* and *R5*, are fixed resistances. Voltage is applied to the bridge from step-down transformer *T1*, and the bridge output is connected to an amplifier. When the bulb temperature changes, the resulting bridge unbalance is amplified to operate a servomotor and move the slide-wire contact to a new position of equilibrium. The position of the contact then represents the temperature at the thermometer bulb.

The calibration equation of the Wheatstone bridge circuit can be derived by setting to zero the expression for its output voltage. Designating e_1 as the voltage applied to the bridge from the transformer *T1*, P the resistance of *R1* and *R2* in parallel, *L1* the resistance of each lead wire, and x the resistance of the fraction of P between the bottom end of the slide-wire and its contact, then for balance

$$\left(\frac{e_1-i_1L_1}{L_1+P+R_3+R_4}\right)(L_1+R_3+x)-\left(\frac{e_1-i_1L_1}{R_6+R_5+L_1}\right)(R_6+L_1)=0 \quad (4)$$

where i_1 is the current in the transformer branch. Defining

$$R_6=R_{01}+r_1 \quad (5)$$

where R_{01} is the resistance of the thermometer bulb at 28 degrees Fahrenheit and r_1 is the change in the resistance from 28 degrees Fahrenheit to the temperature measured, and by constructing the resistances so that

$$R_3=R_{01} \quad (6)$$

and

$$P+R_4=R_5 \quad (7)$$

equation 4 can be rearranged to give

$$x=\frac{R_5r_1}{R_{01}+r_1+L_1+R_5} \quad (8)$$

As e_1 and i_1 do not appear in this equation the calibration is independent of the applied voltage.

The magnitude of the fractional error

caused by a change of lead resistance can be determined from the derived equation

$$\frac{dx}{x} = -\frac{dL_1}{R_{01}+r_1+L_1+R_5} \tag{9}$$

By making the denominator large compared to the expected dL_1, it is possible to keep small the effects of changes in lead length on the calibration. For the circuit values used a change in lead resistance of 2.5 ohms will cause an error of only 0.1 degree Fahrenheit at full scale, and one-half this error at mid scale. This resistance corresponds to approximately 400 feet of number 18 copper wire. By calibrating the 3-lead circuit for a nominal value of lead resistance, large changes in the lead length can be tolerated.

An expression for the resistance of the thermometer bulb at temperature T is

$$R_6 = R_{01}(1+a(T-28)+b(T-28)^2) \tag{10}$$

where a and b are constants for the wire material. If

$$t = T-28 \tag{11}$$

from equations 5 and 10

$$r_1 = R_{01}(at+bt^2) \tag{12}$$

Substituting 12 in 8

$$x = \frac{R_5R_{01}(at+bt^2)}{R_{01}(1+at+bt^2)+L_1+R_5} \tag{13}$$

The slope of x with respect to t is

$$\frac{dx}{dt} = \frac{R_5R_{01}(R_{01}+L_1+R_5)\ (a+2bt)}{[R_{01}(1+at+bt^2)+L_1+R_5]^2} \tag{14}$$

In this equation both the numerator and denominator increase with t, and it is possible by proper selection of R_{01} and R_5 to make the slope practically constant over the full-scale range. The thermometer bulb wire in this instrument is nickel to high purity, and the bridge circuit is designed for this bulb so that the maximum departure of the calibration from a linear scale is only 0.06 degree Fahrenheit.

The measuring sensitivity of the circuit depends on the temperature coefficient of the bulb wire and the current through it. The current used, about 20 milliamperes, is sufficiently low for the bulb construction so that the temperature rise caused by the power dissipated in the winding is negligible. The bulb has a time constant of 0.45 second and consequently gives a response of 90 per cent of the change in one second.

Conductivity Circuit

The conductivity measuring circuit, shown in Figure 7, is a Wheatstone bridge. *R16* is the resistance of the sea water in the cell, *L2* is the resistance of each lead, and *R13*, *R14*, and *R15* are fixed resistances. Transformer *T2* supplies a voltage e_2 to the bridge circuit. The amplifier and servomotor are identical to those used with the temperature measuring system. Designating Q as the resistance of *R11* and *R13* in parallel, and y as the resistance of the fraction of Q between the upper end of the slide-wire and its contact, then, by a treatment similar to that applied to the temperature circuit, it can be shown that

$$y = \left(\frac{Q+R_{14}+L_2}{1+\dfrac{(R_{15}+L_2)c}{k}}\right)\frac{R_{15}}{k}c \tag{15}$$

where c is the specific conductance of the sea water and k is the cell constant, which are related to *R16* by

$$k = c \times R_{16} \tag{16}$$

The circuit values are selected so that y is equal to Q when c is the full-scale value of specific conductance, c_m.

Since the denominator in equation 15 is not constant, the scale distribution is nonlinear. However, as specific conductance is not directly recorded on the linear chart, but used only for computing salinity, linearity is not necessary. The circuit values used in this instrument cause a maximum nonlinearity of less than two per cent.

As in the temperature measuring circuit, the primary element is connected to its bridge by three leads. Here also the purpose of the 3-lead connection is to keep the errors caused by a change in lead resistance to a small value. If only two leads were used, the sum of their resistances would add directly to the resistance of the sea water in the cell. For the circuit values used in the instrument, a length change of 16 feet of two number 18 wires would introduce an error of 0.1 per cent at full scale.

The bridge resistances are constructed so that

$$Q = R_{15} \tag{17}$$

and

$$R_{14} = \frac{k}{c_m} \tag{18}$$

For these relationships it can be shown that the use of three leads instead of two for connecting the cell to the bridge circuit reduces the maximum error caused by a change in lead resistance in the approximate ratio of eight to one. With the circuit values used in the instrument, a change in lead length of about 125 feet will introduce a 0.1 per cent error.

The constant for a conductivity cell depends on its mechanical dimensions and the sizes, shapes, and surface conditions of the electrodes. Cells of similar design can be readily made having constants within two or three per cent of each other. When a cell is replaced by another having a different constant, the value of the resistance *R15* can be changed to retain the

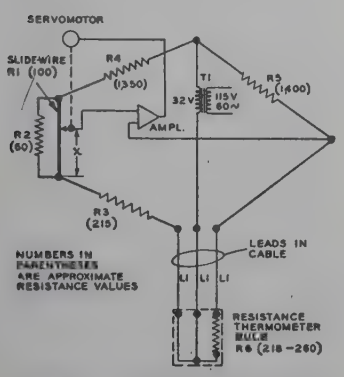


Figure 6. Temperature measuring circuit

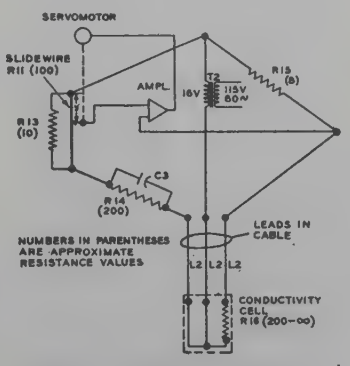


Figure 7. Conductivity measuring circuit

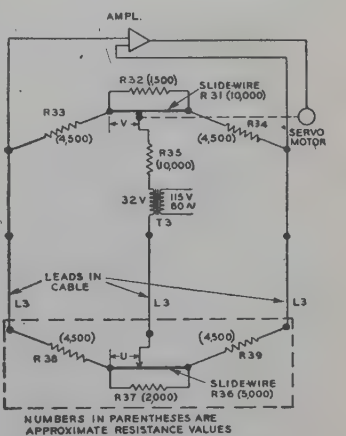


Figure 8. Depth measuring circuit

original calibration for one particular value of specific conductance. For other specific conductances the calibration is altered slightly, the extent of the change depending upon the magnitude of the term $(R_{15}+L_2)/k$ in equation 15. With the circuit components used in the instrument a five per cent change in the value of the cell constant will cause only a 0.08 per cent variation in the calibration curve. Each cell has a separate *R15* resistance spool made for it, and when cells are changed the *R15* spools are also changed.

Another factor affecting the value of the constant of a cell is the phenomenon of polarization, which introduces uncertain errors in the measured conductance. When direct current is passed through a solution, the products of electrolysis accumulate at the electrodes and no constant value of conductance can be determined. With alternating current the ions are not discharged at the electrodes. However, there are still some polarization effects, which are attributed to variations in the ionic concentrations near the electrodes. To obtain good accuracy the effects of polarization must be kept small. This can be accomplished by using a cell with electrodes of large surface area and a large constant and by employing high a-c frequencies. A common method for increasing the effective area of an electrode is the application of a coating of platinum black to its surface. Tests made by Kohlrausch and Holburn[12] indicate that polarization is negligible for platinized electrodes when the area of the electrode in square centimeters is greater than $50 \times C$, whereas 0.1 per cent accuracy can be obtained with bright electrodes whose area is greater than $2{,}500 \times C$, C being the measured conductance expressed in mhos. Experiments by Thuras[4] have shown that the difference in polarization between 1,000 and 60 cycles is quite small, being in the order of 5 parts in 100,000. Because of its availability, and as it permits the use of the same type amplifier employed with the temperature circuit, 60-cycle alternating current is used for the conductivity circuit.

Another effect of polarization is to produce an apparent high capacitance in series with the conductance of the cell. The reactance of this capacitance is in quadrature with the conductance, and it does not change the measured conductance in proportion to its magnitude. However, it does affect the sensitivity of detecting the balance condition of the circuit and it becomes more important at the lower frequencies. Platinization of the electrodes increases the value of the series capacitance, making its reactance smaller. During the experimental stages of the development of this instrument it was observed that for the cell and electrode arrangement used, the ratios of the series capacitances to the conductances were approximately constant for all salinities within the working range. This ratio is the cotangent of the phase angle between the applied voltage and the resulting current. If the phase angle were exactly constant for a cell it would be possible to cancel completely the quadrature component of the circuit output by introducing the capacitor *C3* across the resistance *R14* to shift the phase of the current in the balancing branch of the circuit an equal amount. This capacitance is determined from the relation

$$C_3 = \frac{\tan N}{2\pi f R_{14}} \qquad (19)$$

where N is the phase angle of the cell and f is the frequency. By applying a capacitor in this manner the need for platinum-black coatings on the electrodes was avoided.

Depth Measuring Circuit

The depth measuring circuit, shown in Figure 8, is a double slide-wire bridge. *R36* is the slide-wire in the transmitting unit, the contact of which is positioned by the free end of a helical pressure spring. *R37*, *R38*, and *R39* are fixed resistances in the transmitter. *R31* is the slide-wire in the recorder, whose contact is actuated by a servomotor and mechanically connected to the depth recording pen. *R32*, *R33*, *R34*, and *R35* are fixed resistances in the recorder. The resistance of each lead is indicated by *L3*. Transformer *T3* applies a voltage e_3 to the bridge, and the amplifier unit amplifies any unbalance and causes the servomotor to move the recorder contact to restore a condition of balance. In a conventional bridge of this type the amplifier is normally connected between the two sliding contacts, rather than as shown in Figure 8. With a high-input impedance amplifier this arrangement has the advantages of providing uniform sensitivity over the scale range and being unaffected by large changes in the

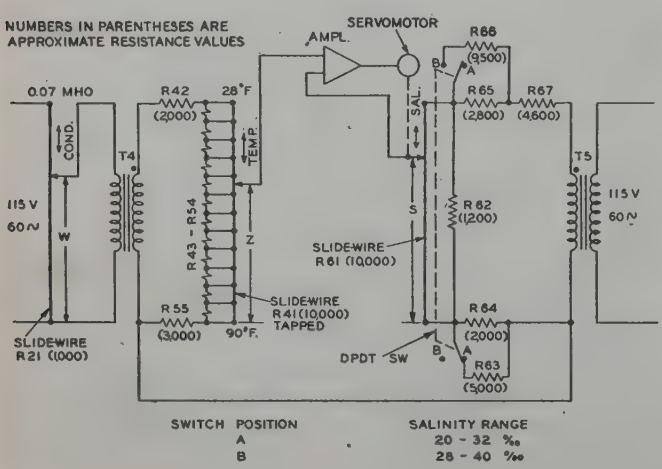


Figure 9. Salinity computing circuit

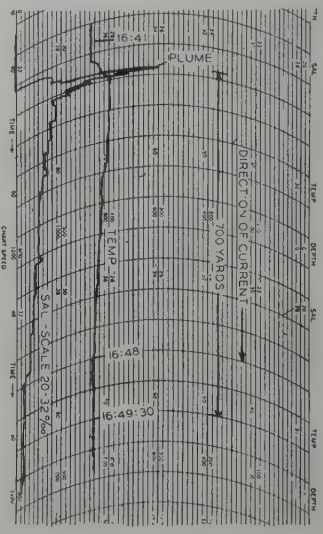


Figure 10. Surface recording in vicinity of sewer outfall at New Bedford, Mass.

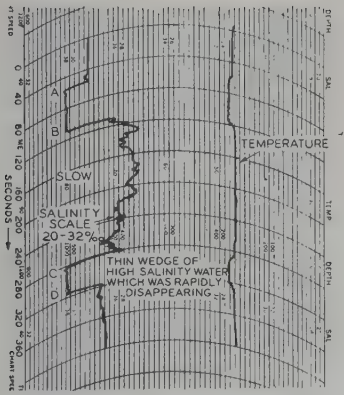


Figure 11. Surface recording in Mount Hope Bay

contact resistances. However, as the lead to the transmitter contact is in the long cable connecting the measuring elements assembly to the recorder, it is subject to inductive effects from the currents and voltages of the adjacent leads connecting to other circuit elements. These can directly introduce errors in the depth measurements, depending upon the amplitude and relative phase of the resultant pickup. To avoid this possibility of error, the voltage supply is connected between the two sliding contacts. Here, the same degree of pickup in the cable lead has a negligible effect because of the relatively large measuring current flowing in it. This is consistent with the connections of the temperature and conductivity circuits, where the amplifier input leads which are sensitive to pickup are all in the on-board equipments, and can be kept short and be properly shielded. This arrangement has the disadvantage of causing variable measuring sensitivity over the depth scale and less protection against variations in the contact resistances. However, by making the resistance of *R35* high, and the effective resistances of the slide-wires low, in relation to the resistances on each side of the slide-wires, these disadvantages become negligible. By doing this there is considerable attenuation of the useful power, but as the total power supplied to the bridge is small this is not a serious matter.

Designating the parallel resistance of *R31* and *R32* by *M*, the parallel resistance of *R36* and *R37* by *N*, with *v* and *u* representing the fractions of *M* and *N* respectively, from the left-hand end of each slide-wire to its contact, and by constructing the resistances so that

$$M = N \tag{20}$$

and

$$R_{32} = R_{34} = R_{38} = R_{39} \tag{21}$$

then the contact position at balance is given by

$$v = \frac{(2R_{32} + M)u + ML_3}{2(R_{33} + L_3) + M} \tag{22}$$

For this circuit arrangement, the maximum error caused by a change in lead resistance can be shown to be represented by

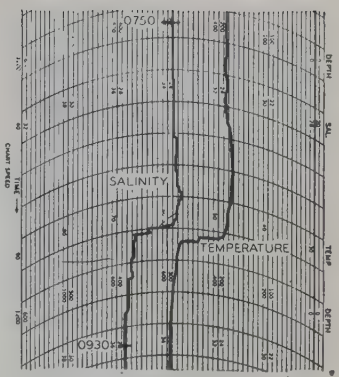
$$\frac{dv}{M} = \frac{dL_3}{2R_{32} + M} \tag{23}$$

Thus, by making the denominator large, the effects of changes in the lead resistance will be small. In the instrument this value is 10,000 ohms, so that a 1-ohm change in lead resistance (160 feet of number 18 wire) will cause a maximum error of only 0.01 per cent.

The depth elements for the different ranges are made interchangeable by setting the fixed resistances associated with each element in accordance with the relations indicated in equations 20 and 21.

Salinity Computing Circuit

Figure 9 is a diagram of the circuit used for computing salinity from the simultaneous measurements of conductivity and temperature. Slide-wire *R21* is connected across the line, and its movable contact is positioned from the shaft of the conductivity unit according to a specific function of conductivity. The current in the temperature compensating slide-wire *R41*, connected to the secondary of transformer *T4*, is proportional to this same function, and its contact is positioned by the shaft of the temperature unit. The output voltage of *R41* is, therefore, proportional to the product of the conductivity and temperature functions. The current in slide-wire *R61* is supplied by transformer *T5*, the primary of which is connected to the power line. The transformers are used only to isolate the computing circuits from the line, each transformer having unity voltage ratio. When the voltage is zero between the contacts on slide-wires *R41* and *R61* the position of the contact on *R61* represents the product of the conductivity and temperature functions given in equation 3, which is the salinity. Any change in this product causes an output voltage, which is amplified, and operates the servomotor to move the *R61* contact to a new position of equilibrium. *R42* through *R55* and *R62* through *R67* are fixed resistances. The switch associated with slide-wire *R61* serves to set the range of the salinity circuit. For the switch position shown the range is 20 to



S.T.D. NO. 2 – 24 APRIL 1947 – CELL AT 3½ FT
TIME: 0750 – 0930
LAT.: 39°26′.1 N — LONG.: 69°55′.1 W
LAT.: 39°16′.6 N — LONG.: 69°52′.7 W
SALINITY SCALE 28-40‰

Figure 12. Surface traverse across edge of Gulf Stream

32‰. The amplifier and servomotor are identical to those used with the other measuring systems.

Designating the resistance of *R41* paralleled by the series resistances *R43* through *R54* by *H*, and the parallel resistance of *R61* and *R62* by *J*, with *w*, *z*, and *s* representing the effective variable resistances, as shown in Figure 10, then it can be shown that the amplifier input is zero when the three contact positions, *w*, *z*, and *s*, are related so that

$$s = \left(R_{67} + R_{65} + J + \frac{R_{64}R_{61}}{R_{63} + R_{61}}\right) \times \left(\frac{w}{R_{21}(R_{42} + H + R_{66}) + w(R_{21} - w)}\right)(R_{66} + z) - \frac{R_{63}R_{61}}{R_{63} + R_{61}} \tag{24}$$

As voltage does not appear in equation 24 the balance position is unaffected by variations in the supply. This equation for *s* can be expressed in simplified form by

$$s = Af_1(w)f_2(z) - B_1 \tag{25}$$

Where *f* indicates the functions of the respective variables and *A* and *B1* are constants. The function of *w* includes the loading effect of the temperature-compensating circuit on slide-wire *R21*, but does not consider the added load of the exciting current of transformer *T4*. This load, which is kept low by using a transformer with a large number of turns, is taken into account in the initial calibration of the instrument.

The contact of slide-wire *R21* is positioned according to the required function of specific conductance and modified for the loading effects by means of a cam asso-

ciated with the output shaft of the conductivity unit. The contact on slide-wire *R41* is moved directly by the output shaft of the temperature unit, and its position is linearly related to temperature. The required function of temperature is obtained by using the proper distribution of effective resistance in the slide-wire. This is accomplished by tapping the linear slide-wire winding at several points and shunting each section separately with a fixed resistance. This method approximates the continuous curve by a series of straight-line sections, the approximation becoming better as more sections are employed. In the instrument 12 sections are used in slide-wire *R41*, which together with the associated shunting resistances, *R43* through *R54*, provide an approximation with a maximum error of 0.05 per cent.

Large changes in the resistances of the contacts on slide-wires *R41* and *R61* are negligible, as they are in series with the high resistance input of the amplifier. A change in the resistance of the contact on slide-wire *R21*, however, will affect the accuracy of the computation because it alters the voltage applied to transformer *T4*. The error resulting from this condition can be minimized by making the equivalent impedance of the transformer and its load large compared to the resistance of *R21*. No difficulty has been encountered in practice with this arrangement.

The first step in the design of the computing circuit is the selection of a conversion factor relating salinity units to resistance or voltage units. Although this selection is made arbitrarily, the choice of the factor is restricted by consideration of circuit output sensitivity, applied voltage, and the physical properties of the slide-wires. The factor used in the instrument is 80 ohms per part per thousand of salinity.

The salinity range of the chart is determined by the position of the double-pole double-throw switch. Thus, for the position shown, the *B1* constant in equation 25 is equivalent to 20‰. When the switch is in the high-range position

$$B_1 = R_{63} \tag{26}$$

which is equivalent to 28‰. The A constant is then

$$A = R_{67} + \frac{R_{65}R_{66}}{R_{65}+R_{66}} + J + R_{64} \tag{27}$$

The resistances are proportioned so that

$$R_{66} + \frac{R_{63}R_{64}}{R_{63}+R_{64}} = \frac{R_{65}R_{66}}{R_{65}+R_{66}} + R_{64} \tag{28}$$

Thus, the constant A has the same value for both switch positions, maintaining the same current through slide-wire *R61* for each of the salinity ranges.

The parallel arrangement of resistances is used so that the switch contacts will be in series with the high resistance shunts, thus making negligible the effects of varying switch contact resistances.

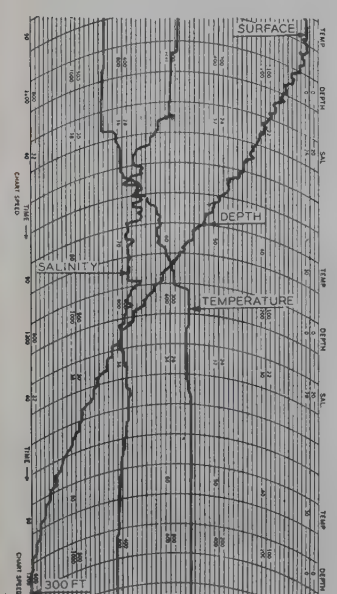
Use at Sea

Several of the salinity-temperature-depth recorders have been made and are being used regularly at sea. An earlier model, which recorded salinity and temperature only, has been in use for nearly three years. These instruments have proved to be well adapted to securing continuous measurements from a moving vessel. For determining surface water conditions, the measuring elements assembly may be mounted on the hull below the water line, where the conductivity cell is irrigated by the boat's motion, or inboard in which case it is irrigated by a stream of water maintained with a pump. When used on a small boat, where the intake is within a few feet of the surface, air bubbles are frequently drawn into the circulation and cause undesirable fluctuations in the salinity record. This difficulty did not appear when the measuring elements assembly was installed on an intake line of the research vessel Atlantis which was located 12 feet below the water line. On small boats it may be overcome by mounting the intake tube on a strut which holds it about one foot away from the hull at a depth of two or three feet.

Figures 10 and 11 are illustrations which show how strikingly the instrument records sudden changes in the temperature and salinity of the surface water. In Figure 10 a record is shown taken from a boat which passed directly over the outfall of the sewer at New Bedford, Mass., in the direction in which the tide was flowing. Note the sharp discontinuity encountered upstream of the outfall, the great drop in salinity as the plume was crossed and the gradual increase in salinity which occurred over a distance of 700 yards downstream. Figure 11 shows a sharp discontinuity in salinity encountered in Mount Hope Bay where a tongue of more saline water had become surrounded by dilute water flowing from the Taunton River. The boat entered the saline water at *A*, crossed into more dilute water at *B*, turned and re-entered the tongue at *C* and emerged from it at *D*.

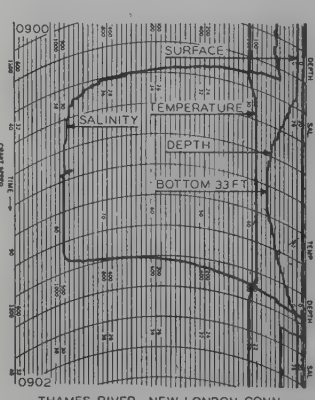
Figure 12 shows a record of the temperature and salinity at a depth of three and one half feet made in a 10-mile traverse across the inshore margin of the Gulf Stream.

Figures 13 and 14 show records of vertical measurements through temperature and salinity gradients. The depth transmitting element used for these surveys was calibrated to give full-scale deflection



LAT.: 39°45'N — LONG.: 70°45'W
AUG. 7, 1947 — BALANUS CRUISE NO.10
S.T.D. NO.1 — DEPTH SCALE 0-300'
SALINITY SCALE 28-40‰

Figure 13. Vertical recording in ocean water



THAMES RIVER, NEW LONDON, CONN.
S.T.D. NO. 2-3 APRIL, 1947 — 0900 — 0902
DEPTH SCALE 0-300 FT
SALINITY SCALE 20-32 ‰

Figure 14. Vertical recording in Thames River Estuary at New London, Conn.

of the depth recording pen for 300 feet. The true depths are obtained from the records by dividing by two the readings on the 0–600 scale. These records indicate clearly the usefulness of the instrument for obtaining the hydrography of complicated water structures. It can be noted from Figure 13 that the temperature and salinity are reasonably constant from the surface to a depth of 50 feet, indicating a well-mixed layer. From 50 to 200 feet both the temperature and salinity undergo large changes, but the gradients are not uniform. Below 200 feet both quantities are reasonably constant. The considerable wiggle in the depth trace was caused by the rolling of the vessel. Note how the magnitude of the wiggle is reduced with increasing depth, as the sag in the lengthening cable absorbs the vertical motion of the boat.

Figure 14 shows the very sharp salinity gradient in the estuary of the Thames River at New London, Conn. A shallow layer of fresh water from the river overlays the more saline water from the Long Island Sound. From both the large positive salinity gradient and the negative temperature gradient it is evident that a large positive density gradient exists, indicating a very stable water column with little tendency for vertical mixing.

Experience has indicated the need for taking certain precautions in using the instrument. It was anticipated that serious errors in the measurements of conductivity might result from fouling of the cell with bacterial slime of macro-organisms. A cell has been operated under the wharf at Woods Hole for weeks at a time. Under these conditions the cell constant slowly changes, causing a salinity error of as much as $0.5^0/_{00}$. Under active use during surveys difficulties due to fouling have not arisen, but it is clear that the measuring elements should not be mounted permanently where they are inaccessible to cleaning or are subject to fouling over prolonged periods. Some difficulties caused by inadequate flushing of the conductivity cell have been encountered in vertical surveys, making it necessary to exercise care in controlling the rate of descent of the measuring elements. Further study is being given the cell design with the object of improving its flow characteristic. Improved accuracy over limited ranges of the measured quantities can be obtained by taking calibration samples of water within the ranges and applying fixed corrections to the records.

Conclusions

A practical salinity and temperature recording instrument is described. This type of instrument has been operated regularly for more than three years and has been found useful for obtaining hydrographic data. It has been applied particularly for inshore surveys in shoal water and in ocean areas where its accuracy of 0.2 degree Fahrenheit and $0.3^0/_{00}$ is adequate. Its time constant of one-half second permits continuous records of temperature and salinity to be made from a moving vessel, or while the measuring elements are being lowered vertically.

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Contribution No. 429

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FORAMINIFERA OF A SUBMARINE CORE FROM THE CARIBBEAN SEA

BY

FRED B. PHLEGER, JR.

COMMUNICATED MARCH 8, 1948

Contribution No. 429 from the Woods Hole Oceanographic Institution

GÖTEBORG 1948
ELANDERS BOKTRYCKERI AKTIEBOLAG
Printed in Sweden

Introduction

During August, 1947, the writer was a guest of the Swedish Deep Sea Expedition aboard the ALBATROSS on its journey through the Caribbean Sea from Martinique, F. W. I., to Cristobal, C. Z. One of the principal purposes of this visit was to observe the operation of the new submarine coring tube developed by Dr. Börje Kullenberg. At the suggestion of Professor Hans Pettersson, Director of the Expedition, 75 samples were taken from the long Core 34 for the purpose of studying the vertical faunal variations of the Foraminifera. The writer greatly appreciates the privilege of studying the material from this core and also the able assistance in sampling the core aboard the ALBATROSS.

Core 34 is 15.4 meters in length and is from ALBATROSS station 30 in the Caribbean Sea at N. Lat. 14° 25′, W. Long. 65° 55′, and from a depth of 2677 fathoms. The top several centimeters were in a fluid condition and apparently the top sample, the surface of the bottom sediment, was not present. The fact that the top sample was absent became obvious when the Foraminifera were examined. Since the coring tube was not completely filled with material, it is presumed that this top layer was lost.

The purpose of this study is to make a reconnaissance of the planktonic Foraminifera faunas to determine whether any environmental changes are suggested by these faunas, and also to determine, if possible, how far back into geologic time this core is projected. Samples were taken at variable intervals to coincide with apparent differences in lithology of the core material. Each sample is a complete cross-section of the core either 1 cm. or 1/2 cm. in thickness. This was cut out with a fine steel wire and all borders of each sample were generously trimmed to avoid contamination by Foraminifera foreign to the fauna.

The position of each sample is given in Table 1 in terms of distance in centimeters from the top of the tube. In measuring these distances the writer has assumed that the coring tube was full, although this was not the case. It seems probable that the tube

Table 1. Positions of the samples in Albatross Core 34.

Sample	Distance from Top of Core in cm.	Sample	Distance from Top of Core in cm.	Sample	Distance from Top of Core in cm.
3401 a	33— 34	3408 a	515— 516	3418 a	1 210—1 211
3401 b	47— 48	3408 b	543— 544	3418 b	1 243—1 244
3401 c	69— 70	3408 c	559— 560	3419 a	1 284—1 285
3402 a	93— 94	3409	590— 591	3419 b	1 314—1 315
3402 b	115—116	3410 a	652— 653	3419 c	1 329—1 330
3402 c	139—140	3410 b	699— 700	3420 a	1 338.5—1 339
3403 a	160—161	3411 a	720— 721	3420 b	1 350—1 350.5
3403 b	176—177	3411 b	745— 746	3420 c	1 359—1 359.5
3403 c	201—202	3411 c	762— 763	3420 d	1 373—1 373.5
3404 a	222—223	3412 a	790— 791	3420 e	1 387—1 387.5
3404 b	241—242	3412 b	839— 840	3420 f	1 339.5—1 400
3404 c	261—262	3413 a	869— 870	3421 a	1 411.5—1 412
3404 d	279—280	3413 b	904— 905	3421 b	1 416—1 416.5
3405 a	303—304	3414 a	934— 935	3421 c	1 425—1 425.5
3405 b	349—350	3414 b	943— 944	3421 d	1 433.5—1 434
3406 a	371—372	3414 c	979— 980	3421 e	1 441—1 441.5
3406 b	394—395	3415 a	1 031—1 032	3421 f	1 447—1 447.5
3406 c	419—420	3415 b	1 049—1 050	3422 a	1 512—1 512.5
3407 a	437—438	3416	1 078—1 079	3422 b	1 519—1 519.5
3407 b	486—487?	3417 a	1 157—1 158	3422 c	1 539—1 540
3407 c	489—490	3417 b	1 189—1 190		

was full when it was taken and that the upper several centimeters of material was unavoidable spilled in handling the core sampler aboard ship. Moreover, it was not possible to obtain an accurate position for the top of the material in the tube because of its fluid condition.

The Foraminifera

The Foraminifera are almost exclusively of planktonic species, a characteristic of the faunas deposited in the deep ocean basins. Since this is a preliminary study the planktonic species only have been identified and used. The approximate relative abundance of the species are recorded in Table 2 in terms of percent of the entire planktonic assemblage of each sample. The percentages listed are approximately correct, and certainly represent the correct order of magnitude in each case. They are determined by counting only a

small fraction of all samples except those which contain only a small number of specimens. A quartering method is used which is believed to give a fair representation of the relative distribution of the species.

The total number of specimens was estimated for each sample. These figures give a rough index of the abundance of Foraminifera at various times since each sample represents approximately the same amount of core material. In giving the number of specimens for samples which were only 1/2 cm. in thickness the actual population figures have been doubled so that they will compare with the majority of the samples.

There is some uncertainty in identifying any but large, and presumably adult, specimens of many of these species. *Globigerina eggeri* is here used for a species to which the names *G. concinna*, *G. dubia*, and *G. conglomerata* have been used by various authors. It is at present believed that *G. eggeri* is the correct name to apply to this species. Specimens here assigned to *G. pachyderma* are rather small and some of the specimens may belong to another species. There is the possibility that some of the specimens assigned to *Globorotalia scitula* may be young stages of *G. crassa*. In the lower samples in the core many specimens were arbitrarily assigned to *Globorotalia menardii* although they appear to be intermediate in structure between *G. menardii* and *G. tumida*. Many of the percentages of *Globigerina bulloides* may be too high, since numerous small and presumably juvenile specimens were assigned to this species. This is suspected further because the percentages of *G. bulloides* appear to the writer to be somewhat high for material collected in such low latitudes.

Interpretations of the faunas in this core in terms of relative approximate water temperatures are given graphically in plate 1. The uppermost sample contains a fauna of somewhat different composition from that now living in the Caribbean Sea and it appears to represent somewhat cooler water conditions than those now obtaining in this area. Sample 3401 b has a definite very cool temperate aspect, with no Globorotalidae and other warm water types, and containing an abundance of *Globigerina bulloides*, *Globigerinoides rubra* and several specimens of *Globigerina pachyderma* or a related form. Sample 3401 c contains a fauna indicative of warmer water than the top sample. This tropical fauna occurs down to sample 3403 c, at 200 cm., with the exception of sample 3402 b, at 115 cm., and 3403 a, at 160 cm., both of which may represent cooler conditions.

From 200 to 242 cm. there is a fauna which is transitional between warm and cold conditions. Between 242 and 763 cm. there are at least five separate coldwater faunas separated by faunas clearly indicative of much warmer waters. The intervening warmer water faunas in this section of the core are of the general type which are at present found in temperate latitudes, while the cold water faunas in this section appear to be similar to those at present living in sub-Arctic areas of the Atlantic.

Below 763 cm. there is a temperate fauna which grades downward into a tropical fauna at 869 to 905 cm. Below this there is a subtropical assemblage from 934 to 980 cm. and a rather cool temperate assemblage between 1 031 and 1 079 cm. Samples 3417 a at 1 157 cm., and 3418 a at 1 210 cm., contain cold water faunas and they are separated by a warm water fauna in sample 3417 b at 1 189 cm. Beneath this there is a relatively thick section of warm water, probably subtropical, faunas from sample 3418 b at 1 243 cm., to sample 3420 c at 1 359 cm. The lower section of the core contains three cold water faunas: samples 3420 d at 1 373 cm., 3421 a at 1 411 cm., and 3422 a at 1 512 cm. They are separated by two tropical assemblages. In the lowest part of the core the fauna suggests a swing from cold conditions to warmer water.

There were certain samples and groups of samples in this core which contained a very high percentage of broken and somewhat eroded specimens; this occurrence is shown in figure 1. The breakage was not due to the process used in preparation of the samples for study since most of the samples contained little or no broken material. The specimens were broken and partially eroded either during or after deposition. The significance of these layers of broken material is not apparent to the writer.

Discussion

It is believed that the relative temperature interpretations of these various faunas in Core 34 are approximately correct, although some details are open to question. The vertical faunal variations in this core are as sharply delineated as any seen by the writer and better than most. It is certain that the various assemblages represent rapidly changing ecologic conditions and it appears that temperature is perhaps the most important of the factors.

There are many more vertical temperature variations indicated in this core than in any previous submarine core studied, to the best of the writer's knowledge. Eleven obvious shifts to cold water faunas have been recorded and it is possible that even more would have been discovered if the sampling had been more detailed. It is apparent that the times of colder water were associated with the various glacial stages of the Pleistocene. It is not possible at the present time to interpret with certainty this sequence of shifting marine conditions in terms of Pleistocene history since our knowledge of the marine phases of the Pleistocene is scanty. It appears possible however that the numerous shifts to cold water conditions are to be correlated with the various substages of the glacial epochs. It is not possible to determine exactly which substages are represented but it seems likely that all of them would be recorded and preserved in the faunas contained in deep sea sediments.

It is interesting to speculate upon possible correlations of the sequence in this core with the known Pleistocene sequence in North America. The thick midsection of the core which contains a tropical or subtropical fauna, from about 762 to 1 000 cm., may be considered to represent a long period of warm conditions, assuming that the rate of sedimentation was uniform throughout the core. This certainly represents an interglacial stage, probably either the Second Interglacial or the Third Interglacial.

If this thick warm water fauna is the Second Interglacial, as seems possible, then the material lying above about 762 cm. represents the Illinoian, the Third Interglacial, Wisconsin, and post-Glacial times. In this case the Third Interglacial may be considered to be represented by the rather thick deposit of temperate faunas between 437 and 516 cm. According to this interpretation there would then be 4 or 5 glacial substages represented in the Wisconsin, at samples 3406 c (419 cm.), 3405 b (349 cm.), 3404 c (261 cm.), possibly 3402 b (115 cm.), and 3401 b (47 cm.). Post-glacial time would be only partially represented by the top sample recovered. The Illinoian stage would be represented between about 530 and 750 cm. It would contain two definite cold periods represented by the cold water faunas between samples 3408 b and 3410 a (543 to 652 cm.) and in sample 3411 b (745 cm.).

Below the Second Interglacial, on this interpretation, there are five glacial stages or substages. The First Interglacial may be represented by the fairly thick, generally subtropical fauna between

samples 3418 b and 3420 c (1 243 to 1 359 cm.). There are then two substages in the Kansan represented by the cold water faunas in samples 3417 a (at 1 157 cm.) and 3418 a (at 1 210 cm.). The Nebraskan contains at least three substages represented by the cold water faunas in samples 3420 d at 1 373 cm., 3421 a at 1 411 cm., and 3422 a at 1 512 cm., and there may be more cold water faunas not penetrated by the core.

It is not yet possible to accurately estimate the rate of deposition of deep water marine sediments, but suggestive estimates can be made. On the basis of the thickness of postglacial sediments in the South Atlantic basin, SCHOTT (1935) has estimated deposition rate at approximately 1 cm. in 1 000 years. About the same rate can be obtained from the thickness of postglacial sediments in two submarine cores from the North Atlantic basin described by PHLEGER and HAMILTON (1946). PIGGOT and URRY (1942) suggest a rate of 0.5 to 1 cm. per year for a core from the Caribbean. The rate is approximately 2 cm. per 1 000 years in one core from the Gulf of Mexico briefly described in a preliminary report by TRASK, PHLEGER, and STETSON (1947); the rate of deposition in the Gulf of Mexico basin should be higher than in the Caribbean because of large additions of detritus from the Mississippi drainage.

If a rate of deposition of 1 cm. in 1 000 years is taken for the Caribbean Sea core, and if it is assumed that this rate was constant, it is possible to estimate the length of time represented by these sediments. At this rate, 1 540 cm. would represent a time of approximately 1 500 000 years. This is of the same order of magnitude as time estimates which have been made for the Pleistocene, although larger than most. It thus appears quite possible that the above interpretation of four glacial stages and numerous substages may be essentially correct for the present core.

It is also possible to assume that the thick section of tropical and subtropical fauna from 762 to 980 cm. was accumulated during the Third Interglacial. On this assumption there would be six or seven cold water faunas in the Wisconsin stage, representing perhaps as many substages. The lower five cold water faunas might then be assigned to Illinoian time. With a constant sedimentation rate of 1 cm. in 1 000 years, the length of time represented by the latter half of the Pleistocene would be approximately 1 500 000 years, with perhaps twice as much time for the entire Pleistocene. The interpretation of four glacial and three interglacials appears to the

writer to be the more reasonable explanation in the light of our present knowledge of the Pleistocene. On either interpretation several substages are suggested for two or more of the glacial stages, and it is possible that additional substages would be suggested if more detailed sampling were done. There is no evidence that Core 34 penetrated into pre-Pleistocene sediments, but it is strongly suggested that it may have obtained most of the Pleistocene at this place. It must be emphasized that the interpretations given above are quite hypothetical and are open to further verification or disproof.

The results from this long core have opened new possibilities for the study of middle and early Pleistocene sequence in marine sediments. The collection of additional long cores from the Caribbean Sea should add greatly to our knowledge of the Pleistocene, and should aid in solving many of the problems raised by the present study. Long cores already obtained by the Swedish Deep Sea Expedition should contain important clues to marine history.

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Tryckt den 27 oktober 1948.

Contribution No. 430

Reprinted from THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA, Vol. 20, No. 3, 271–276, May, 1948
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Secondary Pressure Pulses Due to Gas Globe Oscillation in Underwater Explosions I. Experimental Data*†

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Pressure waves emitted by the oscillating gas globe in underwater explosions of T.N.T. have been recorded at depths great enough to render small the perturbation effects due to migration of the bubbles under the influence of gravity. The first eight periods of oscillation have been measured and the pressure-time curves analyzed in order to obtain peak pressure, positive impulse, and energy flux resulting from the first two pulses. The scaling of pressure pulse parameters with charge size is examined.

I. INTRODUCTION

1.1. The detonation of an explosive charge results in the conversion of the initial solid material into a globe of gaseous products at exceedingly high temperature and pressure. This is followed by expansion of the gas globe and propagation of a strong shock wave through the fluid medium surrounding the charge.

In underwater explosions, the succeeding phenomena are associated with the oscillation of the gas globe, which expands to a maximum radius and then collapses under the influence of the hydrostatic pressure. A pressure pulse (called the first bubble pulse) is emitted while the bubble is near minimum size, and second, third, etc. bubble pulses are emitted as the bubble proceeds with successive oscillations. A typical pressure-time curve for the entire phenomenon is reproduced in Fig. 1.

1.2. The gas globe produced in an underwater explosion tends to migrate vertically upwards under the influence of gravity, the migration being most pronounced in the interval when the bubble is near its minimum radius. In the process of migration, some of the potential energy is converted into kinetic energy of vertically moving water. This energy is not restored to the bubble as it collapses, and hence the amplitude of the emitted pressure wave is less than it would have been had no migration occurred. This effect does not scale with charge size in the same way as other parameters because of the constancy of the acceleration of gravity, g.

From the foregoing, it is evident that the pressure pulse will be at a maximum under conditions which make the bubble migration negligible or cause the bubble to be in a "rest position." It is known that for relatively small charges a rest position occurs at a certain critical depth below the water surface owing to the balancing of gravitational effects by the repulsion from the free surface.[1] However, accurate pressure-time measurements under these circumstances are not possible because proximity to the free surface causes serious interference from the surface reflection of the pressure wave.

Since migration decreases with increasing depth of detonation, it is possible, by performing experiments at sufficiently great depths, to make the migration effects relatively small, or in some cases completely negligible, and thus determine the parameters of the bubble pulse unperturbed by the effects of nearby surfaces and bubble migrations.

1.3. The object of the present investigation was to obtain such unperturbed measurements in order to test the scaling of bubble pulse parameters with charge size and to obtain better impulse and energy flux data than have hitherto been available for the stationary bubble.

Cast T.N.T. was used in three charge sizes: 0.505 lb., 2.507 lb., and 12.01 lb. Measurements

* This work was performed under contract NOrd 9500 with the Navy Department, Bureau of Ordnance.
† Contribution from the Woods Hole Oceanographic Institution No. 430.
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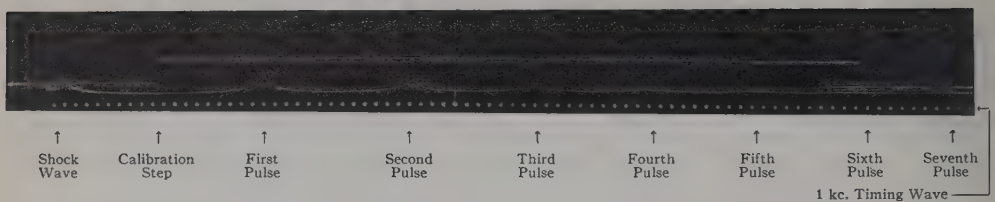

FIG. 1. Pressure-time record showing shock wave and bubble pulses. Charge: 0.505 lb. T.N.T.; Gauge dist.: 2.25 ft. Depth: 500 ft.

were made at a depth of 500 ft. in water having an over-all depth in excess of 650 ft. (For comparison several 0.505- and 2.507-lb. charges were fired at 250 ft.) Under these conditions, surface and bottom effects were negligible. The half-pound charge is deemed to be the smallest T.N.T. charge which can be reliably detonated under these circumstances. The twelve-pound charge is the largest that could be tolerated at a distance of 500 ft. below the vessel performing the experiments; thus, the range of charge size was the widest attainable with the available experimental equipment and with T.N.T. as the explosive.

All pressure-time measurements were made at a distance from the charge such that the value of $W^{\frac{1}{3}}/R$ was constant and equal to 0.352, W being the charge weight in pounds and R the charge to gauge distance in feet. A typical pressure-time record is reproduced in Fig. 1. Periods of pulsation have been measured to the seventh and, in some cases, to the eighth bubble pulse. Peak pressures, impulse, and energy flux have been obtained for the first and second pulses.

II. PERIODS OF OSCILLATION

2.1. Theoretical analysis shows[1] that to a first approximation the period of oscillation of a gas globe is given by

$$T = KW^{1/3}/Z_0^{5/6}, \qquad (1)$$

where K = constant of proportionality, W = charge weight, and Z_0 = absolute hydrostatic depth.

If the energy associated with the oscillation were constant (i.e., if there were no dissipation or acoustic radiation), the period would also remain constant. However, appreciable energy is lost, principally in the neighborhood of the bubble minimum owing to the emission of the pressure wave and other dissipative effects and, consequently, the period of successive oscillations decreases. A summary of the experimental results is given in Table I in terms of the proportionality constant, K, defined by Eq. (1).

2.2. It will be noted in Table I that the values of K_1 for the 2.5- and 12-lb. charges are significantly lower than those for the 0.5-lb. charges. The reproducibility of the period measurements and the fact that charge sizes were alternated in a definite sequence during the shooting program make it very unlikely that the difference is due to systematic experimental error in the measurement of T or Z. The discrepancy can be interpreted only as a slight but significant departure from the ideal cube root law of variation of period with charge weight. (Although correction has been made for the effect of the tetryl booster present in each charge, one cannot be certain of the accuracy of the correction, and it is therefore possible that the observed discrepancy may be due to the relatively larger proportion of booster in the half pound charges.)

Examination of K_n as a function of n shows that the period drops off sharply during the first three oscillations and then decreases slowly but steadily in such a way that the results do not yield a value of K which could be regarded as an accurate limiting value, applicable to the ultimate small amplitude oscillations of the gas globe.

III. PEAK PRESSURE: FIRST AND SECOND PULSES

3.1. Peak pressures of the first and second bubble pulses are summarized in Table II.

As will be indicated in Section V, the cylindrical charges were oriented with their axes in a horizontal plane. Pairs of gauges were placed above, below, and to the side of the charge in positions denoted by $G1$, $G4$, and $G2,3$, respec-

TABLE I. Summary of period constants for T.N.T. $T_n = K_n W^{1/3}/Z_0^{5/6}$, T_n = period of nth oscillation (sec.), W = charge weight (lb.), Z = depth of charge below surface (ft.), Z_0 = absolute hydrostatic depth = $Z+33$ (ft.).

W (lb.)	Z (ft.)	Period constant, K_n							
		K_1	K_2	K_3	K_4	K_5	K_6	K_7	K_8
0.505	250	4.36±.01*	3.14±.03	2.56±.02	2.38±.03	2.16±.04	2.08±.04	1.96±0.1	—
0.505	500	4.36±.01	3.06±.01	2.51±.01	2.32±.01	2.15±.02	1.97±.02	1.90±.02	1.9±.1
2.507	250	4.27**	3.11	2.53	2.35	2.25	2.02	1.94	—
2.507	500	4.26±.01	3.06±.01	2.48±.01	2.31±.01	2.17±.01	2.02±.01	—	—
12.01	500	4.29±.01	3.19±.01	2.56±.01	2.39±.01	2.16±.01	2.04±.01	1.94±.02	1.73±.05

* The stated error is the standard deviation of the mean.
** The error is not indicated since only two shots were made under these conditions. Results of the two shots agreed very closely.

tively, all the gauges being positioned off the cylindrical surface of the charge. It was assumed that the difference between the average pressures at $G1$ and $G4$ was due only to displacement of the bubble toward $G1$, and the pressure was assumed to vary inversely as the gauge to bubble distance. This treatment neglects any effects resulting from possible asymmetry of the pressure field, but it appears to be justified by the fact that when pressures at $G1$ and $G4$ are corrected to the same distance as the $G2,3$ position, all the values agree within experimental scatter.

The values given in Table II are the averages of pressures measured at all three positions and corrected (by means of the apparent migration result) to the given distance from the center of the bubble, $R = W^{\frac{1}{3}}/0.352$ ft.

Because of uncertainty as to the exact location of the true base-line of zero excess pressure on the individual photographic records, the records were read with respect to an arbitrary base-line and were then adjusted to the theoretical baseline value calculated by means of the theory summarized by Friedman.[1] This is based on a calculation of the negative pressure (below surrounding hydrostatic level) existing at the time of the first bubble maximum, and for the conditions represented in Table II the values are -80 and -120 lb./in.^{2} at depths of 250 and 500 ft., respectively.

3.2. Ideal scaling would require that all the peak pressure values at a given ratio of $W^{\frac{1}{3}}/R$ be equal regardless of charge size. Examination of Table II shows that this is not the case. The principal cause of the observed variation is undoubtedly the migration of the bubble. Theoretical calculation of the influence of migration on peak pressure[1] predicts very much less effect than is observed, the expected decrease in peak pressure for the worst case (2.5 lb. at 250 ft.) being less than 1 percent, whereas Table II indicates 15 percent, if ΔP for the half-pound charges at 500 ft. is used as a basis of comparison. Further discussion of this result will be found below in Section IV.

3.3. The results summarized in Table II indicated that the pressure field was cylindrically symmetrical with respect to the axis of the charge. A number of shots were fired with the charge so placed that gauges in position $G2$ faced the cap end while gauges at $G3$ faced the butt end of the charge. Gauges at $G1$ and $G4$ were still above and below the charge, respectively. In Table III the pressures at $G2$ and $G3$ are compared with the pressure at $G2,3$ (off the cylindrical surface) given in Table II. It will be noted that a marked degree of asymmetry exists, particularly in the case of the small charges, with the pressure from the cap end being significantly higher than the pressure from the butt end.

IV. POSITIVE IMPULSE AND ENERGY PULSE

4.1. For convenience in describing and working with various portions of the continuous

TABLE II. Apparent bubble migration and corrected peak pressures. ΔP_n = excess peak pressure of nth pulse (lb./in.^{2}), R = distance from bubble center of point where ΔP_n is measured; $R = W^{\frac{1}{3}}/0.352$ (ft.), W = charge weight (lb. T.N.T.), Z = depth of charge below surface (ft.), Δh_n = vertical displacement of center of bubble from initial charge position at time of nth bubble minimum (ft.).

W (lb.)	Z (ft.)	ΔP_1 (lb./in.^{2})	Δh_1 (ft.)	ΔP_2 (lb./in.^{2})	Δh_2 (ft.)
0.505	250	1120±16*	0.32	225±5	0.51
2.507	250	1020±10	0.80	215±5	1.12
0.505	500	1210±10	0.11	250±5	0.16
2.507	500	1160±10	0.32	245±5	0.47
12.01	500	1140±10	0.86	260±5	0.79

* Stated error is standard deviation of the mean.

TABLE III. Bubble pulse peak pressures for various charge orientations. Notation for position of measurement: *G*2,3—gauge facing cylindrical surface of charge, *G*2—gauge facing cap end of charge, *G*3—gauge facing butt end of charge. Gauge distance from center of bubble: $R=W^{1/3}/0.352$ (ft.), W=charge weight (lb. T.N.T.), ΔP_n = excess peak pressure of nth pulse (lb./in.²).

W (lb.)	Z (ft.)	ΔP_1(lb./in.²)			ΔP_2(lb./in.²)		
		*G*2	*G*2,3	*G*3	*G*2	*G*2,3	*G*3
0.505	500	1365	1210	1095	285	250	230
2.507	500	1200	1160	1150	280	245	240
12.01	500	1200	1140	1120	295	260	250

pressure-time curve illustrated in Fig. 1, an arbitrary subdivision has been adopted. The shock wave is defined as that portion of the curve lying between the shock front (where the time, $t=0$) and the point of first bubble maximum ($t=T_1/2$). Similarly, the first bubble pulse is the portion between first and second bubble maxima, i.e., $T_1/2<t<T_2/2$, etc.

4.2. The impulse delivered by the pressure wave during a fixed interval of time is defined:

$$I=\int_{t_a}^{t_b}\Delta p\,dt. \qquad (2)$$

During a bubble pulse, the pressure is initially negative, becomes positive, and then again negative. It can be shown from acoustic theory that the integral in Eq. (2) taken over the entire pulse as defined above must be very nearly equal to zero. (Actually, there is a small negative residual.) Of principal interest, however, is the magnitude of the positive impulse, the integral being taken only over the region of positive pressure. A summary of average positive impulse values is given in Table IV.

4.3. Impulses measured at *G*1 vertically above the charge are systematically high and those at *G*4 below the charge are systematically low, as would be expected on the basis of the migration results given in Table II. As with the peak pressure (Table III), the impulse is higher at points off the cap end and lower off the butt end than off the cylindrical surface of the charge.

Using the *G*2,3 position (off the cylindrical surface) as being representative of the unperturbed impulse, it is seen that at each depth the impulse scales according to the ideal similarity law within the experimental precision which is

TABLE IV. Positive impulse: First and second bubble pulses (no correction applied for bubble migration). Distance of point of measurement from center of initial charge position: $R=W^{1/3}/0.352$ ft., W=charge weight (lb. T.N.T.), Z=depth of charge below surface (ft.).

W (lb.)	Z (ft.)	Reduced positive impulse, $I/W^{1/3}$ (lb. sec./in.² lb.$^{1/3}$)									
		First pulse					Second pulse				
		*G*1*	*G*2	*G*2,3	*G*3	*G*4	*G*1	*G*2	*G*2,3	*G*3	*G*4
0.505	250	1.39	—	1.34	—	1.32	0.66	—	0.51	—	0.46
2.507	250	1.43	—	1.33	—	1.22	0.71	—	0.57	—	0.47
0.505	500	1.10	1.22	1.16	1.12	1.15	0.45	0.48	0.44	0.40	0.39
2.507	500	1.11	1.17	1.12	1.04	1.07	0.44	0.46	0.43	0.44	0.40
12.01	500	1.15	1.16	1.17	1.06	1.11	0.51	0.49	0.47	0.46	0.46

* See Section 3.3 and Table III for key to position notation.

of the order of 4 percent. This agreement indicates that the pressure differences noted in Table II are confined to a very narrow region in the immediate vicinity of the peak of the pulse and do not affect the remainder of the pressure-time curve appreciably.

Thus, the effect of migration on peak pressure is more than would have been expected on the basis of the theoretical predictions, but the other parameters of the pressure-time curve remain virtually unaffected. Since the impulse obeys the ideal scaling law, it is presumed that the peak pressure also would if the effect of migration could be reduced still further, but this is not conclusively demonstrated and further measurements would be necessary to test the presumption.

4.4. Theoretical analysis[1] shows that to a first approximation the positive impulse in a bubble pulse would be expected to vary as the inverse sixth root of the absolute hydrostatic pressure at the depth at which the bubble is located. A test of this prediction is given in Table V. Since the quantity $IZ_0^{1/6}/W^{1/3}$ is essentially constant with depth, it is seen that the prediction is confirmed within the available experimental accuracy.

4.5. Integrations of the pressure-time curves were also performed for the purpose of determining the irreversible energy flux which is given by acoustic theory as:

$$F=\frac{1}{\rho_0 c_0}\int_{t_a}^{t_b}(\Delta p)^2 dt,$$

where Δp=excess pressure (lb./in.²), t=time (sec.), $\rho_0 c_0$=acoustic impedance of water (slug ft./in.² sec.), and F=energy flux (in. lb./in.²).

The integration was made over the entire bubble pulse as defined in Section 4.1, including both the positive and negative phases, and the averaged results are summarized in Table VI.

4.6. Energy flux measured at $G1$ vertically above the charge is systematically high and that at $G4$ below the charge systematically low, as would be expected on the basis of the migration indicated in Table II. As with the peak pressure (Table III), the energy flux is higher at points off the cap end ($G2$) and lower off the butt end ($G3$) than off the cylindrical surface ($G2,3$).

First pulse energy flux measured in the horizontal plane off the cylindrical surface ($G2,3$) is appreciably decreased by migration losses only in the most severe case—that of the 2.5-lb. charge at 250 ft. The remaining scatter in this column of Table VI is probably due to experimental error.

4.7. From the successive period measurements given in Table I, it is possible to compute the total energy lost by the bubble during the intervals defining the first and second pulses:

$$(B_n - B_{n+1}) = B_n\left[1-\left(\frac{T_{n+1}}{T_n}\right)^3\right], \qquad (4)$$

where B_n = total energy associated with the nth oscillation; T_n = period on nth oscillation.

Taking B_1 as 490 cal./g. of charge and using the values given in Table I, it is found that the total energy lost by the bubble during the first pulse is 300 cal./g. and during the second pulse 85 cal./g. Assuming spherical symmetry about the center of the charge, the $G2,3$ results of Table VI were converted to obtain the total acoustic energy flowing through a spherical surface having a radius equal to the value of R as defined in that table. The resulting energies for the first two pulses are 120 and 15 cal./g., respectively.

It is evident that the measured acoustic radiation accounts for only a fraction of the total energy loss sustained by the bubble in each case. At this time there exists no concrete evidence pointing to the cause of the unaccounted energy loss, although various speculations have been advanced regarding the role of turbulence, chemical reactions among detonation products, etc.

TABLE V. Variation of positive impulse of first bubble pulse with depth of detonation. Z = depth below surface (ft.), $Z_0 = Z + 33$ (ft.), $I/W^{\frac{1}{3}}$ = reduced impulse at $R = W^{\frac{1}{3}}/0.352$, W = charge weight (lb. T.N.T.).

Z_0 (ft.)	$I/W^{1/3}$ (lb. sec./in.^{2} lb.$^{1/3}$)	$IZ_0^{1/3}/W^{1/3}$
40	1.66*	3.1
283	1.34	3.4
533	1.15	3.3

* Obtained at rest position for 300-g T.N.T.-charge near surface and corrected for surface reflection. This value would be expected to be systematically low.

V. EXPERIMENTAL TECHNIQUES

5.1. The charges used were cylinders of cast T.N.T. boostered with pressed tetryl pellets. The weight of tetryl was converted to an equivalent weight of T.N.T. by multiplying by 1.03 as suggested by the results of various period measurements made at this laboratory. One gram was added to the charge weight to account for the explosive in the engineers special blasting caps which were used to detonate the charges.

5.2. Tourmaline piezoelectric gauges[2,3] were used as the pressure sensitive element. The gauges were $\frac{7}{8}$ inch in diameter and had an average sensitivity of 24 micro-microcoulombs per lb./in.^{2}.

5.3. Eight piezoelectric gauges were mounted on $\frac{3}{16}$-in. steel cable in the plane of a 15-ft. diameter steel ring. The ring was suspended in a vertical plane and the charge was mounted at its center. Pairs of gauges were placed at equal

TABLE VI. Acoustic energy flux: First and second bubble pulses (no correction applied for bubble migration). Distance of point of measurement from center of initial charge position: $R = W^{\frac{1}{3}}/0.352$, W = charge weight (lb. T.N.T.), Z = depth of charge below surface (ft.).

W (lb.)	Z (ft.)	Reduced energy flux; $F/W^{\frac{1}{3}}$ (in. lb./in.^{2} lb.$^{\frac{1}{3}}$)									
		First pulse					Second pulse				
		$G1$*	$G2$	$G2,3$	$G3$	$G4$	$G1$	$G2$	$G2,3$	$G3$	$G4$
0.505	250	161	—	141	—	122	23	—	15	—	11
2.507	250	154	—	125	—	101	28	—	16	—	11
0.505	500	140	164	141	135	136	17	20	17	14	14
2.507	500	138	145	134	131	121	19	20	16	16	13
12.01	500	150	150	142	128	120	24	21	22	17	19

* See Section 3.3 and Table III for key to position notation.

[2] Clifford Frondel, "Construction of tourmaline gauges for piezoelectric measurement of explosion pressure waves," OSRD Report No. 6256; NDRC Report No. A-378.

[3] A. B. Arons and C. W. Tait, "Design and use of tourmaline gauges for piezoelectric measurement of air blast," OSRD Report No. 6250; NDRC Report No. A-372.

distances vertically above, vertically below, and horizontally on each side of the charge.

The center of the charge was in the plane of the ring, and two charge orientations were used: (a) axis of cylinder perpendicular to the plane of the ring, (b) axis of cylinder horizontally oriented in the plane of the plane of the ring.

Dimensions were so chosen that the wire structure supporting the gauges did not come in contact with the bubble and was never damaged or appreciably loosened by the forces of the explosion. This insured against uncertainty in gauge position owing to displacement of gauges by the shock wave.

5.4. The over-all depth of water was measured by means of a fathometer, and all experiments were performed in such depths that the charge was always at least 150 ft. away from the bottom. The depth of the charge was determined by the measured length of suspension cable supporting the ring, the method being very reliable since experiments were performed in a region of negligible tidal currents, and the suspension always hung vertically downward. This is confirmed by the reproducibility of the period measurements given in Table I.

5.5. Continuous 600 ft.-lengths of Simplex (F.O. 5879) signal free coaxial cable were used between the gauges and oscilloscopes, thus avoiding occurrence of spurious cable signal for an interval sufficiently long to allow faithful recording of the first two bubble pulses. Cable effects were further minimized by the relatively high sensitivity of the gauges. The polythene core of the cable rendered negligible any low frequency distortion due to dielectric dispersion. The cables were compensated in accordance with principles discussed elsewhere.[4]

5.6. Recording equipment consisted of eight oscilloscope channels[5] on the schooner "Reliance." In order to avoid low frequency distortion, it was necessary to increase the input impedance of the oscilloscopes by using cathode follower preamplifiers. The final over-all time constant of the recording circuits was about 500 millisec.

A 110-v d.c. motor with variable armature voltage was used to drive the rotating drum cameras. Writing speeds were varied from 125 to 400 millisec. per revolution of the 10-inch circumference drums.

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[4] R. H. Cole, "The use of electrical cables with piezoelectric gauges," OSRD Report No. 4561; NDRC Report No. A-306.

[5] R. H. Cole, D. Stacey, and R. M. Brown, "Electrical instruments for the study of underwater explosions and other transient phenomena," OSRD Report No. 6238; NDRC Report No. A-360.

Contribution No. 431

Reprinted from THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA, Vol. 20, No. 3, 277–282, May, 1948
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Secondary Pressure Pulses Due to Gas Globe Oscillation in Underwater Explosions. II. Selection of Adiabatic Parameters in the Theory of Oscillation*

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(Received January 13, 1948)

A summary is given of the theory of pulsation of a stationary gas globe in an infinite incompressible fluid. If three parameters appearing in the formulation are selected by fitting the equations to three independent experimental results, it is shown that the theory fits the remaining experimental results and can be used to predict bubble pulse properties over wide ranges of the independent variables.

I. INTRODUCTION

1.1. The theory of the pulsation of gas globes formed in underwater explosions has been treated by several investigators during the past few years and has been summarized by Friedman in a recent report of the New York University Institute for Mathematics and Mechanics.[1] The theory in this formulation depends upon three parameters which cannot be accurately determined by means of *a priori* calculations, and recourse must be had to experimental information regarding certain properties of the bubble pulsation.

Experimental results obtained in deep water at the Woods Hole Oceanographic Institution[2] afford the necessary information, and it is the purpose of this report to discuss the selection of parameters which make it possible to fit the theory to the experimental results over a wide range of the primary variables.

II. FORMULATION OF THE THEORY

2.1. The theory referred to above[1] has been set up to treat the general case in which the gas bubble migrates as a result of the combined effects of gravity and the presence of neighboring free and rigid surfaces. A brief summary of the formulation will be given here, modified for application to the special case of the stationary bubble (i.e., negligible migration).

Consider a perfect sphere of radius A expanding at radial velocity A' in an infinite incompressive liquid of density ρ. The total kinetic energy of the fluid external to radius A is given by

$$\mathbf{T}=\int_A^\infty 4\pi R^2\frac{\rho(R')^2}{2}dR=2\pi\rho A^3(A')^2, \quad (1)$$

where the primes denote time derivatives.

The potential energy of the system is

$$U=(4/3)\pi A^3P_0+G(A), \quad (2)$$

where the first term represents energy stored against hydrostatic pressure (P_0 being the absolute hydrostatic pressure at the depth of the bubble center), and the second term represents the internal energy of the gas in the bubble. The zero of internal energy is defined as the infinite limit of adiabatic expansion, thus:

$$G(A)=\int_A^\infty pdV, \quad (3)$$

where the line integral is taken along an adiabatic and V represents the total volume of gas.

It is assumed that the gas approximates ideal behavior:

$$pv^\gamma=k_1, \quad (4)$$

where v is specific volume, k_1 is a constant, and γ is the ratio of heat capacities.

Combining Eqs. (3) and (4),

$$G(A)=k_1M^\gamma\int_{V_A}^\infty\frac{dV}{V^\gamma}=\frac{k_1M^\gamma}{(\gamma-1)A^{3(\gamma-1)}(4\pi/3)^{\gamma-1}}, \quad (5)$$

where M is the mass of gas.

Denoting the total energy associated with the oscillation by E,

$$E=2\pi\rho A^3(A')^2+(4/3)\pi A^3P_0+G(A). \quad (6)$$

* Contribution of the Woods Hole Oceanographic Institution No. 431.

[1] Bernard Friedman, "Theory of underwater explosion bubbles," Institute of Mathematics and Mechanics, New York University, Report No. IMM-NYU 166.

[2] A. B. Arons, J. P. Slifko, and A. Carter, "Secondary pressure pulses due to gas globe oscillation in underwater explosions. I. Experimental data," this Journal.

Following the convention adopted by Friedman,[1] it is convenient to transform to dimensionless variables by using the following scale factors for length and time, respectively:

$$L=(3E/4\pi P_0)^{\frac{1}{3}}, \tag{7}$$

$$C=L(3\rho/2P_0)^{\frac{1}{2}}. \tag{8}$$

Combining Eqs. (5), (6), (7), and (8),

$$a^3\dot{a}^2+a^3+ka^{-3(\gamma-1)}=1, \tag{9}$$

where $a=A/L$, the dot denotes derivative with respect to non-dimensional time, and k is given by

$$k=\frac{k_1P_0{}^{\gamma-1}}{(\gamma-1)\epsilon^\gamma}; \tag{10}$$

ϵ is the bubble energy per unit mass of gas (or original explosive charge).

It will be noted that throughout the following analysis the total energy for a cycle of the oscillation will be considered constant. This is a very close approximation for most of the parameters since appreciable quantities of energy are lost by the bubble only during the very short intervals of time in the neighborhood of the bubble minima. The treatment of the peak pressure of the pulse, however, may be appreciably in error because of this approximation.

2.2. Since the bubble is at maximum or minimum when $\dot{a}=0$, the corresponding maximum and minimum bubble radii are given by the roots of the equation,

$$a^3+ka^{-3(\gamma-1)}-1=0. \tag{11}$$

The non-dimensional maximum radius is the root near unity of the above equation, i.e.,

$$a_M=[1-ka_M{}^{-3(\gamma-1)}]^{\frac{1}{3}}. \tag{12}$$

The actual maximum radius is given by $A_M=La_M$.

The non-dimensional minimum radius is

$$a_m\cong k^{1/3(\gamma-1)}. \tag{13}$$

2.3. Assuming the radius-time curve to be symmetrical about the time of bubble maximum, integration of Eq. (9) gives the non-dimensional period of oscillation,

$$t=2\int_{a_m}^{a_M}\frac{a^{\frac{1}{2}}}{[1-a^3-ka^{-3(\gamma-1)}]^{\frac{1}{2}}}da. \tag{14}$$

The actual period of oscillation is given by $T=Ct$.

Shiffman and Friedman have given a method of obtaining this integral[1] with a high degree of precision. Figure 1 shows a family of curves giving t as a function of k for various values of γ.

2.4. Bernoulli's equation affords a relationship for the excess pressure at points in fluid:

$$\Delta p/\rho=(\partial\varphi/\partial\tau)-\tfrac{1}{2}(\nabla\varphi)^2. \tag{15}$$

Here τ is dimensional time and φ the velocity potential which, in the case of spherically symmetrical incompressive flow, is given by

$$\varphi=A^2A'/R. \tag{16}$$

The second term in Eq. (15) is negligibly small compared with the first. Neglecting this term, the excess pressure is given by

$$\Delta p=\rho(A^2A')'/R=2P_0L(a^2\dot{a})\cdot/3R. \tag{17}$$

An expression for $(a^2\dot{a})\cdot$ can be obtained from the equations of motion; the most convenient method is the application of the Lagrange equation to the energy relation of Eq. (6). The result is substituted into Eq. (17), yielding

$$\Delta p=\frac{P_0L}{R}\left[\frac{a^2\dot{a}}{3}-a+\frac{(\gamma-1)k}{a^{3\gamma-1}}\right], \tag{18}$$

since

$$2(a^2\dot{a})\cdot=a\dot{a}^2-3a+3(\gamma-1)ka^{-3\gamma+1}. \tag{19}$$

When a is at a maximum or minimum, $\dot{a}$ is zero. The excess pressure at bubble maximum becomes

$$\Delta P_M=-\frac{P_0L}{R}\left[a_M-\frac{(\gamma-1)k}{a_M{}^{3\gamma-1}}\right]. \tag{20}$$

Using Eq. (13), the excess pressure at bubble minimum is given by

$$\Delta P_m=\frac{P_0L}{R}\frac{(\gamma-1)}{k^{2/3(\gamma-1)}}\left[1-\frac{k^{1/(\gamma-1)}}{(\gamma-1)}\right]. \tag{21}$$

In Eq. (20) it will be noted that (since γ is of the order of 1.3, k of the order of 0.2, and a_M about 0.9) the first term predominates, the second term representing a relatively small cor-

rection for the internal energy of the gas. Thus the minimum excess pressure is negative relative to the original hydrostatic level, as would be expected, and is not critically dependent upon the equation of state of the gas.

Because of the base line uncertainties in the measurements described in the preceding paper,[2] calculations based on Eq. (20) were used to select a baseline to which the pressure-time records were subsequently referred.

2.5. It is seen from Eq. (17) that the non-dimensional bubble radius a_0 at which Δp is zero is determined by the condition that $(a^2\dot{a})\cdot$ be zero. Applying this condition and eliminating $\dot{a}$ from Eqs. (9) and (19), one obtains

$$4a_0^3 = 1-(4-3\gamma)ka_0^{-3(\gamma-1)}. \tag{22}$$

2.6. The positive impulse I delivered by the pressure wave is defined by

$$I=\int_{a_{01}}^{a_{02}} \Delta p d\tau, \tag{23}$$

where the integration is performed over the region lying between the point at which Δp rises to zero during the collapsing phase and the point at which it again falls to zero on the expanding phase, i.e., between points where the non-dimensional bubble radii are denoted by a_{01} and a_{02}, respectively.

Because of the radiation of acoustic energy, the pressure-time curve is not symmetrical about the peak pressure ordinate. For convenience, therefore, the integral of Eq. (23) will be separated into two parts,

$$I=\int_{a_{01}}^{a_m} \Delta p d\tau+\int_{a_m}^{a_{02}} \Delta p d\tau, \tag{24}$$

where a_m is the non-dimensional minimum bubble radius, i.e., the radius when Δp is a maximum.

Elimination of Δp between Eqs. (17) and (24) and conversion of dimensional time τ to non-dimensional time gives

$$I=\frac{2P_0L_1C_1}{3R}\int_{a_{01}}^{a_m} d(a^2\dot{a}) + \frac{2P_0L_2C_2}{3R}\int_{a_m}^{a_{02}} d(a^2\dot{a}), \tag{25}$$

where L_1 and C_1 are the scale factors of the first and L_2 and C_2 the scale factors of the second bubble oscillation.

Since $\dot{a}$ is zero at the instant of bubble minimum, Eq. (25) becomes

$$I=\frac{2P_0}{3R}[L_1C_1(a^2\dot{a})_{01}+L_2C_2(a^2\dot{a})_{02}]. \tag{26}$$

(In Eq. (26), $\dot{a}$ is understood to represent only the magnitude of the quantity, whereas in Eq. (25) the symbol has an associated algebraic sign.)

The appropriate expression for $(a^2\dot{a})_0$ can be obtained from Eq. (19) by setting $(a^2\dot{a})\cdot$ equal to zero; the result is

$$(a^2\dot{a})_0 = 1.732a_0^2\left[1-\frac{(\gamma-1)k}{a_0^{3\gamma}}\right]^{\frac{1}{2}}. \tag{26a}$$

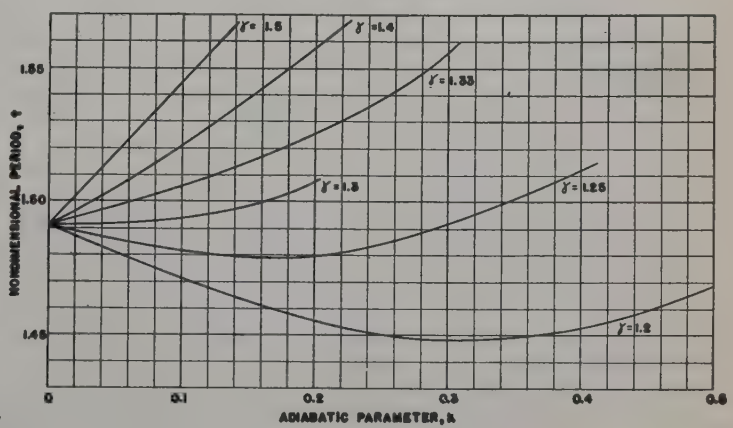


FIG. 1. Non-dimensional bubble period, t, *versus* parameter k for various values of γ.

TABLE I. Comparison of experimental impulse values with calculations based on Eq. (36).

Z_0 (ft.)	$I/W^{\frac{1}{3}}$ (lb. sec./in.^{2} lb.$^{\frac{1}{3}}$) Experimental	From Eq. (36)
40	1.7*	2.0
283	1.33	1.31
533	1.15	1.12

* This value is known to be systematically low because complete correction could not be made for surface reflection effects.

III. SELECTION OF PARAMETERS

3.1. The theory developed in the preceding chapter contains three parameters related to the properties of the gas in the bubble. These are the adiabatic parameters γ and k_1 and the total energy ϵ per unit mass. Although the values of γ, k_1, and ϵ can be estimated roughly on the basis of *a priori* considerations relating to the properties and behavior of the detonation products, such estimates do not lead directly to results of sufficient accuracy to make the theory a means of calculating reliable values of the bubble pulse parameters over reasonably wide ranges of the independent variables.

In order to obtain an empirical fit accomplishing the latter purpose for T.N.T., recourse must be had to the experimental results reported in the preceding paper[2] and to radius-time curves obtained from high speed motion pictures by Dr. J. C. Decius and his co-workers at Woods Hole.

3.2. In general, it is seen from Eq. (14) that the non-dimensional period of oscillation depends on γ and k. Since the latter parameter is a function of the hydrostatic pressure, as given by Eq. (10), one would expect the actual bubble period ($T=Ct$) to deviate from the ideal inverse 5/6 power dependence upon the depth of detonation. Experimental results over a wide range of depth (*ca.* 10 to 500 ft.) indicate that no such deviation is observable within the precision of experimental measurements.

Reference to Fig. 1 shows that the theory would be quite consistent with the above result if the value of γ is taken to be in the neighborhood of 1.25,* since along this curve a wide variation in the value of k has very little effect on the non-dimensional bubble period t. This is equivalent to making t nearly independent of depth and allowing T to vary as $P_0^{-5/6}$ as given by the scale factor C.

3.3. Substitution of the appropriate values in Eqs. (7) and (8) gives the following expressions for the scale factors:

$$L=1.733\epsilon^{\frac{1}{3}}(W/Z_0)^{\frac{1}{3}}, \tag{27}$$

$$C=0.373\epsilon^{\frac{1}{2}}(W^{\frac{1}{3}}/Z_0^{5/6}), \tag{28}$$

where L is in ft., C in sec., ϵ in cal./g, W is charge weight in lb., and Z_0 is absolute hydrostatic depth in ft. If Z is the depth of the charge below the surface, $Z_0=Z+33$.

The experimental data for the first period of oscillation of the T.N.T., bubble is represented by

$$T=4.36W^{\frac{1}{3}}/Z_0^{5/6}. \tag{29}$$

Since $T=Ct$, combination of Eqs. (28) and (29) gives

$$\epsilon^{\frac{1}{2}}t=11.7. \tag{30}$$

It will be seen below that, for the depth range which has so far been accessible, k lies between 0.1 and 0.3. From Fig. 1, t in this range has an average value of 1.483 along the $\gamma=1.25$ curve. Putting this value of t into Eq. (30) gives $\epsilon=490$ cal./g.

3.4. There still remains the problem of selecting the third parameter, k_1. Fitting it to the peak pressure data is the most sensitive method. Expressing P_0 in terms of the hydrostatic depth Z_0, setting $\gamma=1.25$, $\epsilon=490$, and combining Eqs. (7), (10), and (21),

$$\Delta P_m=\frac{3.55(10^7)}{\beta^{2.67}}\frac{W^{\frac{1}{3}}}{R}(1-4k^4), \tag{31}$$

where ΔP_m=excess peak pressure, lb./in.^{2}, W=charge weight, lb., ϵ=bubble energy, cal./g, $k=\beta Z_0^{\gamma-1}/(\gamma-1)\epsilon^{\gamma}$, Z_0=absolute hydrostatic depth, ft., R=radial distance from bubble center, ft.

The term $(1-4k^4)$ in Eq. (31) represents a correction factor which differs from unity by only three percent at depths as great as 1000 ft. It can therefore be disregarded for all practical purposes. The parameter β represents a numerical factor in the general expression for k, and β must be selected in such a way as to provide a fit to the experimental peak pressure data.

* This value is identical with the one obtained by Jones in Britain as a result of the theoretical study of the composition of the detonation products and their equilibrium during the early stages of the bubble expansion.

Measurements of ΔP_m for the first bubble pulse in deep water under conditions of very small bubble migration give values[2] of about 1200 lb./in.^{2} at $W^{\frac{1}{3}}/R=0.352$. Using this result in Eq. (31) gives $\beta=31.8$, and the general expression for the peak pressure becomes

$$\Delta P_m=3450\frac{W^{\frac{1}{3}}}{R}(1-4k^4), \qquad (32)$$

and k is given by

$$k=0.0552Z_0^{\gamma-1}. \qquad (33)$$

IV. APPLICATION TO OTHER MEASUREMENTS

4.1. In the preceding section, experimental period and peak pressure results were used to determine the values of the three arbitrary parameters appearing in the theory. It is now necessary to ascertain whether the same parameters will also fit the rest of the available experimental data, consisting of (a) the maximum bubble radius, (b) the time and corresponding bubble radius at which $\Delta p=0$, and (c) the positive impulse in the first bubble pulse.

4.2. High speed motion picture measurements of T.N.T. bubbles give the maximum bubble radius as

$$A_M=12.6(W/Z_0)^{\frac{1}{3}}, \qquad (34)$$

where A_M is expressed in ft. This represents the average of a large number of measurements over a wide range of depths (*ca.* 100 to 600 ft.). The accuracy of the measurement is believed to be about ± 2 percent, and within this scatter there seems to be no systematic variation with depth of the numerical constant 12.6 in Eq. (34). The experimental non-dimensional maximum bubble radius, a_M, is therefore constant and equal to 0.92 if ϵ is taken as 490 cal./g in calculating the scale factor.

The theoretical values of a_M obtained from Eq. (12) vary from 0.94 to 0.90 for the range of depths cited above. This predicted variation is not confirmed experimentally, but since it is small and of the order of the magnitude of the experimental error, the agreement between experiment and the theoretical fit can be considered quite satisfactory.

4.3. The pressure-time curves[2] which yielded the value of ΔP_m used in the preceding section, also provided measurements of the time (measured from the shock front) at which the excess pressure dropped to zero during the initial bubble expansion and the time at which it returned to zero from the negative phase as the bubble proceeded to collapse. When compared with radius-time curves obtained from high speed motion pictures, these data show the non-dimensional bubble radius a_0 to be 0.62 when $\Delta p=0$. Within the precision of measurement, this value appears to be independent of charge size and depth of detonation.

The corresponding theoretical value of a_0 is obtained by solving Eq. (22) using $\gamma=1.25$ and k as given by Eq. (33). It is found that a_0 is very insensitive to variation in the depth and has values of 0.62 to 0.61 over the range $Z_0=83$ to 533 ft. This is in excellent agreement with the experimental observation of 0.62.

4.4. The positive impulse delivered in the first bubble pulse can be computed from Eqs. (26) and (26a), providing an adequate assumption can be made concerning the magnitude of the scale factors L_2 and C_2. Both of these factors depend upon $\epsilon_2^{\frac{1}{3}}$, and ϵ_2 is known to be less than ϵ_1, owing to the radiation of acoustic energy associated with the emission of the bubble pulse. If period measurements are adopted as the criterion, one would expect as a first approximation that

$$(\epsilon_2/\epsilon_1)^{\frac{1}{3}}=T_2/T_1. \qquad (35)$$

Experimental results give $T_2/T_1=0.72$ as an average.

Thus Eq. (26) can be rewritten

$$I/W^{\frac{1}{3}}=11.9Z_0^{-1/6}(W^{\frac{1}{3}}/R)(1-1.59k)^{\frac{1}{3}}, \qquad (36)$$

γ having been set equal to 1.25 and a_0 to its average value of 0.615 as determined above; the assumption is made that to a first approximation $(a^2\dot{a})_{01}$ is equal to $(a^2\dot{a})_{02}$.

In Eq. (36), $I/W^{\frac{1}{3}}$ = reduced positive impulse (lb. sec./in.^{2} lb.$^{\frac{1}{3}}$), Z_0 = absolute hydrostatic depth (ft.), W = charge weight (lb.), R = radial distance from bubble center (ft.), and $k=0.0552Z_0^{\gamma-1}$.

A comparison of experimental values[2] of $I/W^{\frac{1}{3}}$ with those calculated from Eq. (36) is given in Table I for various depths Z_0. It will be noted that the agreement is quite satisfactory.

4.5. From Eq. (13) it is also possible to make a theoretical prediction concerning the minimum

bubble radius. Combining Eq. (13) with the expression for k, the non-dimensional minimum radius becomes

$$a_m = 0.0210 Z_0^{\frac{1}{3}}, \tag{37}$$

and the dimensional minimum radius,

$$A_m = 0.286 W^{\frac{1}{3}}, \tag{38}$$

where Z_0 = absolute hydrostatic depth (ft.), A_m = minimum radius (ft.), and W = charge weight (lb.).

Unfortunately there is no direct experimental evidence available to check Eq. (38), since the bubble minimum cannot be measured on the high speed motion pictures owing to obscuration by carbon particles, etc. left behind in the water.

V. SUMMARY

5.1. It has been demonstrated in the preceding sections that if the parameters γ, ϵ, and k are set equal to 1.25, 490 cal./g, and $0.0552 Z_0^{\gamma-1}$, respectively, the theoretical equations provide a satisfactory fit to all the available experimental data. This fact increases the utility of the theory in that it should now be possible to make reasonably accurate predictions of stationary bubble behavior under various circumstances, and the same parameters should apply to Friedman's more general theory[1] which includes effects resulting from migration and the influence of neighboring surfaces.

It should be emphasized, however, that any detailed physical interpretation of the parameters γ and k is tenuous at best. It is somewhat surprising that so satisfactory a fit to the peak pressure and impulse data can be obtained with the same parameters which fit the maximum bubble radius and period data. One would expect, for example, the true pressure-volume relationship to deviate appreciably from the ideal gas adiabatic which was used in the theoretical formulation, and the deviation would be most pronounced during the high pressure, high temperatures phase in the neighborhood of the bubble minimum.

In view of the multitude of approximations and assumptions involved, it would appear to be more rational to regard the numerical values of γ and k as parameters affording a useful fit of simplified theory to experimental results rather than as actual physical properties of the detonation products. The distinction may appear to be subtle, but it is probably significant.

VI. ACKNOWLEDGMENTS

6.1. The author wishes to express his gratitude to Dr. J. C. Decius and Dr. B. Friedman for permission to reproduce the curves of Fig. 1 and to the Underwater Explosive Research Laboratory, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts where all the experimental data quoted in this report were obtained.

Contribution No. 432

Reprinted from the JOURNAL OF MORPHOLOGY
Vol. 82, No. 2, March, 1948

STUDIES ON DEEP-SEA ANGLER-FISHES (CERATIOIDEA)

III. THE COMPARATIVE ANATOMY OF GIGANTACTIS LONGICIRRA WATERMAN [1]

TALBOT HOWE WATERMAN
Osborn Zoological Laboratory, Yale University, New Haven, Connecticut

TEN FIGURES

I. INTRODUCTION

The structure and organic functions of even so highly specialized a vertebrate as a modern spiny-finned fish show a striking conservatism in their basic plan. But this fundamental pattern is overlain by a palimpsest of idiosyncrasies and innovations. Their analysis in terms of the history of the individual organism and the animal group to which it belongs offers a stimulating challenge. Much of the recent work in this field, like Wald's ('46) studies on the phylogeny of the vitamins A, has been comparative biochemical or comparative physiological in approach. Yet numerous morphological problems remain unattacked despite their broad interest for many fields of biology. Particularly the examination of puzzling anatomical questions in the light of modern knowledge of physiology, embryology, and evolution might be expected to yield answers which, in turn, would catalyze further progress in these diverse fields.

[1] This work was begun during the author's tenure of a Fellowship at the Woods Hole Oceanographic Institution (Contribution no. 432), and continued in part while he was an Austin Teaching Fellow and Junior Fellow of the Society of Fellows, Harvard University.

The present paper is one of a series whose aim is to demonstrate these generalizations with the deep-sea angler-fishes *(Ceratioidea)*. It treats particularly of *Gigantactis longicirra* Waterman ('39b), which belongs to the *Gigantactinidae* Boulenger ('04), a specialized family of this aberrant teleost suborder.

II. BACKGROUND

The deep-sea angler-fish are members of the Order *Pediculati,* so-called from the arm-like structure of the pectoral fins. This order ranks serially as one of the last in the classifications of teleosts used by most ichthyologists. Berg ('40), for example, places his Order *Lophiiformes* (= *Pediculati* Regan, '12) as no. 113 out of the 114 orders in which he classifies recent and fossil fishes. The group certainly represents one of the distal branches of actinopterygian radiation.

Like the rest of the pediculates, the ceratioids have the first rays of the spinous dorsal located on the skull and modified into an illicium. It is believed to act as a lure for attracting the fish's prey within striking distance of the mouth. In these deep-water forms, which live in perpetual darkness, the terminal bait, or esca, of the illicium is illuminated by a light organ under the control of the animal. No ceratioid has been observed using its illicium for angling, but the organ's use for the purpose is inferred by analogy with its shallow-water relatives, like *Lophius* and *Antennarius,* which a number of workers have studied alive (for discussion, see Waterman, '39a, p. 68).

The oral and pharyngeal cavities of ceratioids are relatively enormous, and many of their other anatomical features are also conditioned by an overall adaptation as "animated fish-traps." The bony skeleton is typically reduced and the musculature, particularly for swimming, is weak. Pelvic fins are lacking in the suborder and the pectorals, although they retain the basic pediculate structure with elongate radial bones, are reduced in size and scope of movement.

Unlike other pediculates, deep-sea anglers are bathypelagic in habit. In keeping with this they have strongly developed

black or dark brown pigmentation and the light producing organ of their fishing apparatus. The eyes are small. Certainly the most bizarre characteristic of these fishes is the presence, in certain of them at least, of dwarf parasitic males which become grown fast to the surface of the females. The anatomy of the known parasitic and free-living male ceratioids is quite different from that of the females, which have largely formed the basis for the generalizations about the group. This relationship between the sexes is unique among the vertebrates. Adequate knowledge of its physiological and phylogenetic significance must await further study.

Although less than 1000 specimens of ceratioids are listed in the literature, these have been classified into nearly 200 species distributed among 11 families. The *Gigantactinidae* comprise a family to which 11 species (10 in the Genus *Gigantactis)* have been assigned (Regan and Trewavas, '32; Waterman, '39b; Beebe and Crane, '47). The number of known specimens totals but 12! This would certainly suggest that natural selection is operating at a very low rate on these fishes, at least within the group, but lack of adequate data prevents any real analysis of the situation.

Gigantactis longicirra is known from only a single specimen (39 mm in standard length). In deference to its being a type, the facts given here were obtained from a detailed dissection of just one side of the fish, which was caught in a closing net at 1000 m (bottom was at 2860 m) about 300 miles east of Cape May, New Jersey (Waterman, '39b, p. 82). In the course of the work, which was carried out with the specimen in alcohol and under a dissecting microscope, drawings of each point of interest were made as it was revealed. Photographs, camera lucida, and projections methods were used wherever they seemed desirable for insuring accuracy. The final figures were assembled and redrawn from the notes and study sketches after the dissection had been completed.

These studies were initiated before the war and have only now been completed after a 6-year interruption by war research.

III. SYSTEMATIC ANATOMY

Since the accompanying figures present the anatomy of *Gigantactis* in considerable detail, the verbal account in this section will serve mainly to emphasize the more significant points and indicate the broad generalizations. In the succeeding section (IV) the implications of these facts for comparative anatomy and morphogenesis will be analyzed.

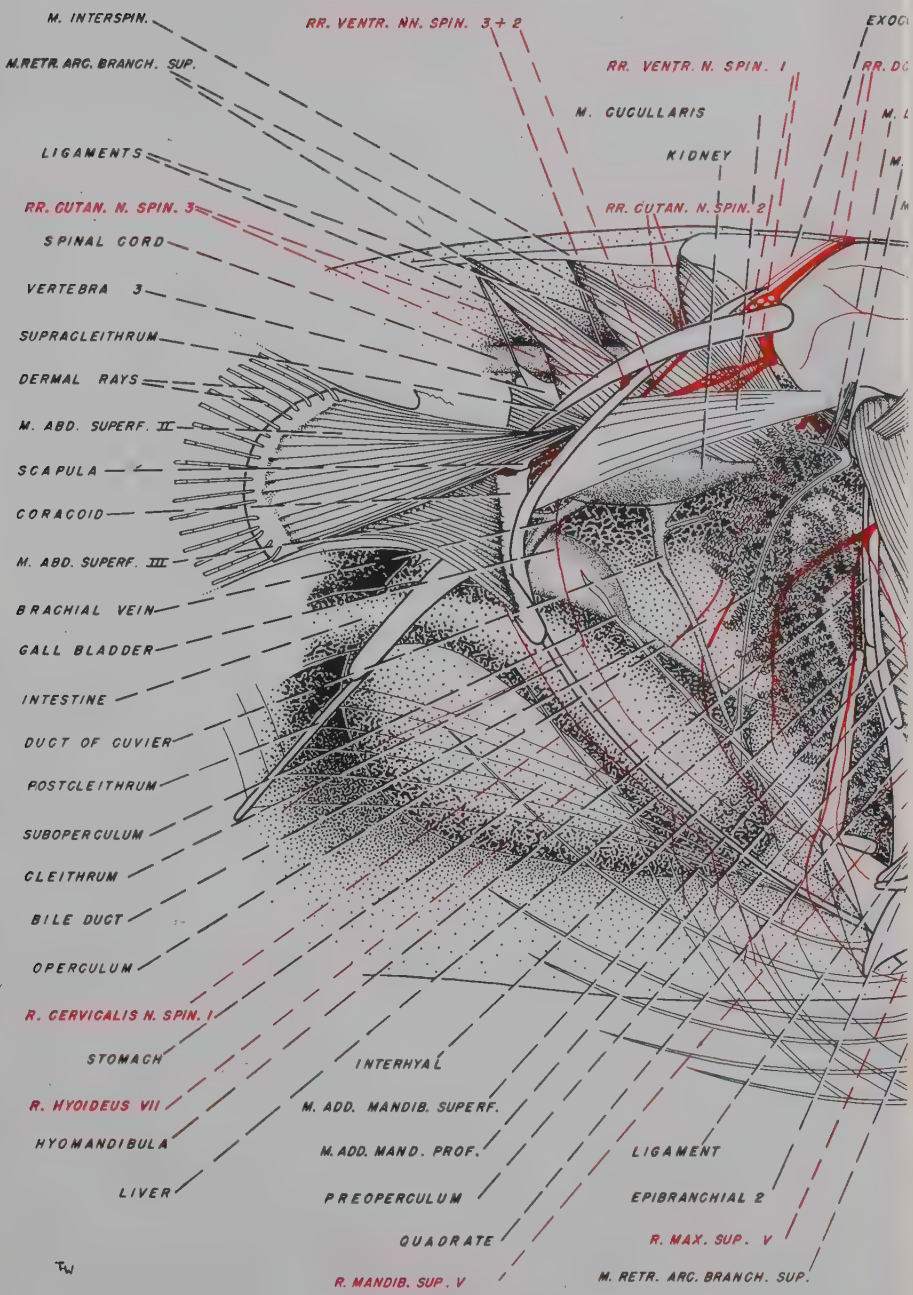
A. Body form

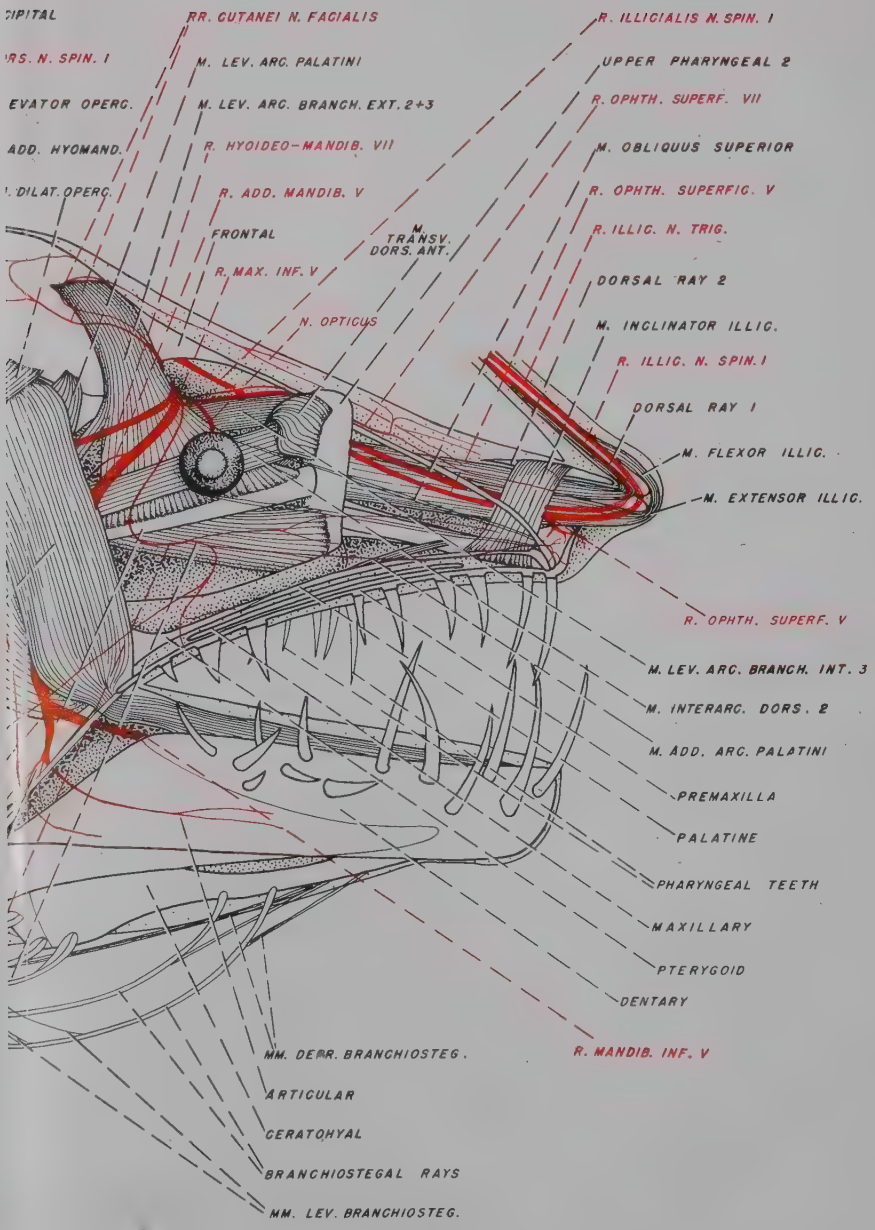
With its elongate and slim body *Gigantactis* is more streamlined than most ceratioids (Waterman, '39b, fig. 1). The lateral musculature is weakly developed and the median fins, particularly the caudal, have long trailing fin rays. The pectorals, which are of a reduced pediculate type, arise far back on the body and high on its sides well above the longitudinal axis of the body.

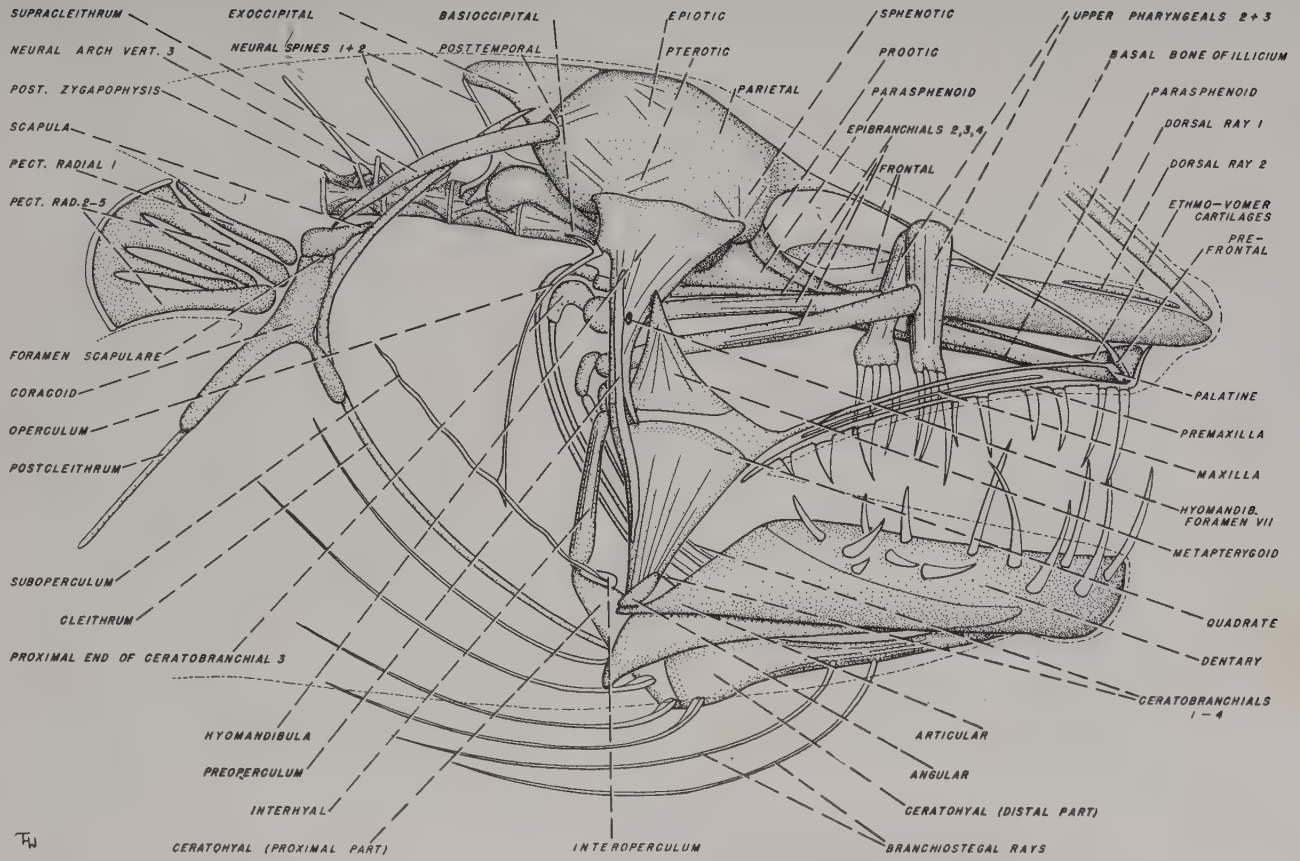
The head, although reduced in depth and width relative to that of nearly all ceratioids, still forms a dominant part of the body (fig. 1). Distance from snout to posterior of the bow of the cleithrum [2] exceeds 30% of the standard length. The long illicium emerges terminally from the attenuated snout. The mouth, subterminal in position, has a large gape and is plentifully provided with sharp piercing teeth. The hyomandibular suspension lies almost vertically and by its length depresses the quadrate-articular joint considerably. Nevertheless, the elongation of the snout and the shape of the jaws combine to direct the mouth forward and only slightly upward rather than markedly dorsad as in forms like *Melanocetus, Ceratias,* or *Muncalias* (see Regan and Trewavas, '32,

[2] The subbrachial respiratory exit and the vestigial opercular bones in this fish make the usual teleost head measurement to the posterior margin of the operculum rather meaningless.

Fig. 1 General anatomy of *Gigantactis longicirra* Waterman. × 10. Lateral view of anterior half of the type specimen after skin and superficial connective tissue had been dissected away. Standard length of the fish 39 mm. Nervous system in red.


M. INTERSPIN.
M. RETR. ARC. BRANCH. SUP.
LIGAMENTS
RR. CUTAN. N. SPIN. 3
SPINAL CORD
VERTEBRA 3
SUPRACLEITHRUM
DERMAL RAYS
M. ABD. SUPERF. II
SCAPULA
CORACOID
M. ABD. SUPERF. III
BRACHIAL VEIN
GALL BLADDER
INTESTINE
DUCT OF CUVIER
POSTCLEITHRUM
SUBOPERCULUM
CLEITHRUM
BILE DUCT
OPERCULUM
R. CERVICALIS N. SPIN. I
STOMACH
R. HYOIDEUS VII
HYOMANDIBULA
LIVER
RR. VENTR. NN. SPIN. 3 + 2
RR. VENTR. N. SPIN. 1
M. CUCULLARIS
KIDNEY
RR. CUTAN. N. SPIN. 2
INTERHYAL
M. ADD. MANDIB. SUPERF.
M. ADD. MAND. PROF.
PREOPERCULUM
QUADRATE
R. MANDIB. SUP. V
LIGAMENT
EPIBRANCHIAL 2
R. MAX. SUP. V
M. RETR. ARC. BRANCH. SUP.


CIPITAL
RS. N. SPIN. 1
EVATOR OPERC.
ADD. HYOMAND.
DILAT. OPERC.
RR. CUTANEI N. FACIALIS
M. LEV. ARC. PALATINI
M. LEV. ARC. BRANCH. EXT. 2+3
R. HYOIDEO-MANDIB. VII
R. ADD. MANDIB. V
FRONTAL
R. MAX. INF. V
N. OPTICUS
M. TRANSV. DORS. ANT.
R. ILLICIALIS N. SPIN. 1
UPPER PHARYNGEAL 2
R. OPHTH. SUPERF. VII
M. OBLIQUUS SUPERIOR
R. OPHTH. SUPERFIC. V
R. ILLIC. N. TRIG.
DORSAL RAY 2
M. INCLINATOR ILLIC.
R. ILLIC. N. SPIN. 1
DORSAL RAY 1
M. FLEXOR ILLIC.
M. EXTENSOR ILLIC.
R. OPHTH. SUPERF. V
M. LEV. ARC. BRANCH. INT. 3
M. INTERARC. DORS. 2
M. ADD. ARC. PALATINI
PREMAXILLA
PALATINE
PHARYNGEAL TEETH
MAXILLARY
PTERYGOID
DENTARY
R. MANDIB. INF. V
MM. DEPR. BRANCHIOSTEG.
ARTICULAR
CERATOHYAL
BRANCHIOSTEGAL RAYS
MM. LEV. BRANCHIOSTEG.


SUPRACLEITHRUM
NEURAL ARCH VERT. 3
POST. ZYGAPOPHYSIS
SCAPULA
PECT. RADIAL 1
PECT. RAD. 2–5
FORAMEN SCAPULARE
CORACOID
OPERCULUM
POSTCLEITHRUM
SUBOPERCULUM
CLEITHRUM
PROXIMAL END OF CERATOBRANCHIAL 3
HYOMANDIBULA
PREOPERCULUM
INTERHYAL
CERATOHYAL (PROXIMAL PART)
EXOCCIPITAL
NEURAL SPINES 1+2
BASIOCCIPITAL
POSTTEMPORAL
EPIOTIC
PTEROTIC
PARIETAL
INTEROPERCULUM
SPHENOTIC
PROOTIC
PARASPHENOID
EPIBRANCHIALS 2,3,4
FRONTAL
UPPER PHARYNGEALS 2+3
BASAL BONE OF ILLICIUM
PARASPHENOID
DORSAL RAY 1
DORSAL RAY 2
ETHMO–VOMER CARTILAGES
PRE–FRONTAL
PALATINE
PREMAXILLA
MAXILLA
HYOMANDIB. FORAMEN VII
METAPTERYGOID
QUADRATE
DENTARY
CERATOBRANCHIALS 1–4
ARTICULAR
ANGULAR
CERATOHYAL (DISTAL PART)
BRANCHIOSTEGAL RAYS

on the snout. Correlated with this is an elongation of the preoptic region of the skull and the formation in it of a longitudinal trough in which the basal bone of the illicium lies (fig. 3A). The sphenoid elements are elongate so that the ethmo-vomer block is carried forward to form the base for the rostral part of this cradle. The frontals, prefrontals, palatines, maxillaries, and premaxillaries are correspondingly attenuated to form slender skeletal strands.

Anteriorly the long illicial trough is made possible by the absence of roofing elements in the skull forward of the otic capsule. Posteriorly the trough is bounded by the supra-occipital. This forms the antero-medial wall of the otic region by virtue of its marked concavity to accommodate the posterior end of the basal bone of the illicium. These relations contradict the diagnostic feature given for the *Gigantactinidae* by Regan ('26, p. 37), namely, that the illicial trough extends the whole length of the skull. This it certainly does not do in *Gigantactis longicirra;* furthermore, the structure described in *Gigantactis gracilicauda* (Regan, '26, fig. 12) as mesethmoid (and later called parasphenoid, Regan and Trewavas, '32, p. 38) shows very different proportions and relations to the rest of the skull in the present specimen.

Within this excavation of the fore skull the basal bone of the fishing filament lies nearly horizontally. Its posterior end rests against the floor of the trough while the anterior portion is propped up by the forward part of the ethmo-vomer region

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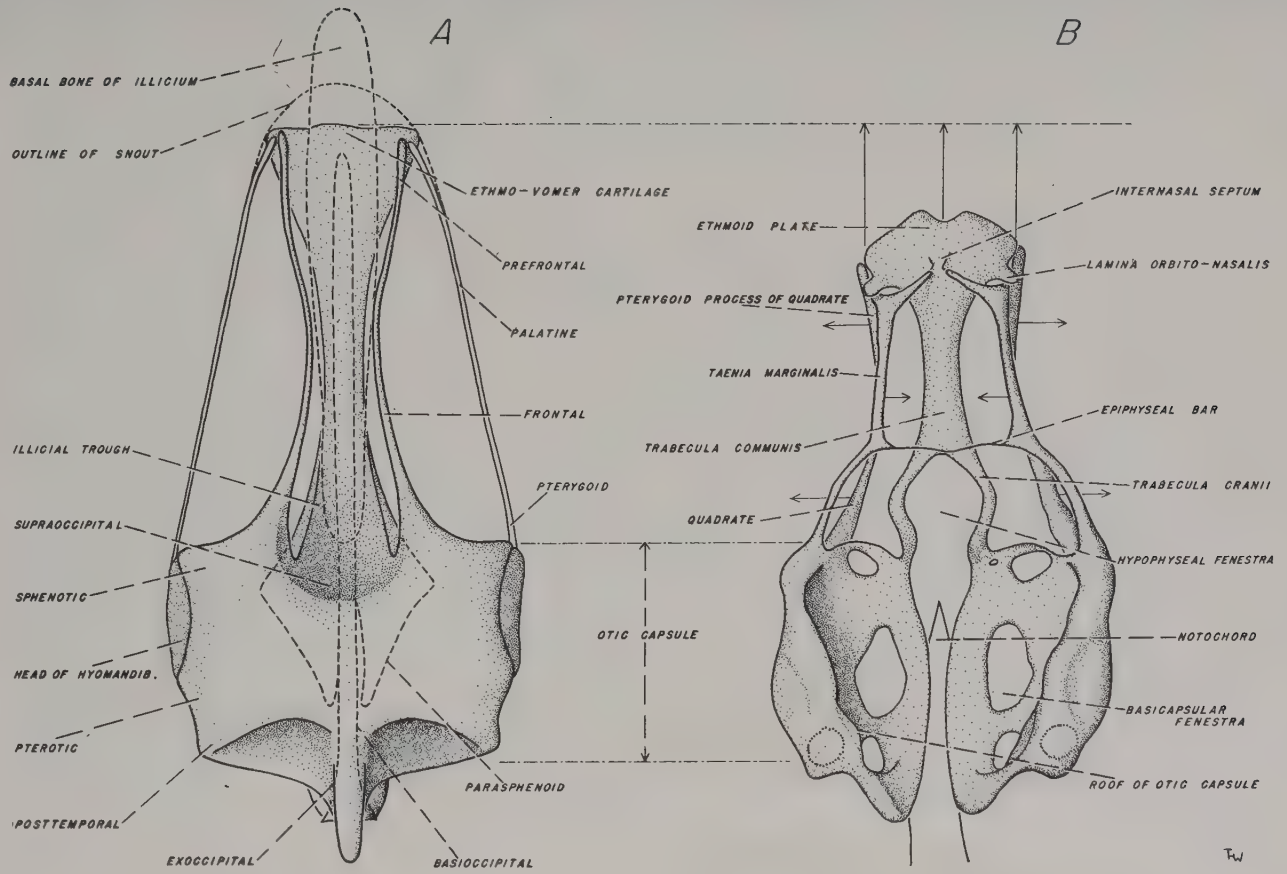
Fig. 3 Comparison of crania of *Gigantactis* and larval *Salmo fario*. See text pp. 43 ff. for analysis.

A. Dorsal view of skull of *Gigantactis*. × 10. Rerefence to figures 1 and 2 will demonstrate the importance of the vacuities visible in this view between the frontal-prefrontal and palatine-pterygoid elements; the specialized upper pharyngeals are displaced forward and upward into these openings and with their associated muscles largely fill up the space so created.

B. Dorsal view of chondrocranium of *Salmo fario* 9 days after hatching, 16.5 mm long. × 25. Redrawn from de Beer, '27, text figure 38. Three sets of arrows suggest morphological changes which would produce cranial proportions even more like those of *Gigantactis*. The factors apparently determining in the angler-fish such deformations from the basic teleost pattern are discussed in the text.


A
B
BASAL BONE OF ILLICIUM
OUTLINE OF SNOUT
ETHMO-VOMER CARTILAGE
PREFRONTAL
PALATINE
FRONTAL
ILLICIAL TROUGH
PTERYGOID
SUPRAOCCIPITAL
SPHENOTIC
HEAD OF HYOMANDIB.
PTEROTIC
POSTTEMPORAL
EXOCCIPITAL
BASIOCCIPITAL
PARASPHENOID
OTIC CAPSULE
ETHMOID PLATE
INTERNASAL SEPTUM
LAMINA ORBITO-NASALIS
PTERYGOID PROCESS OF QUADRATE
TAENIA MARGINALIS
EPIPHYSEAL BAR
TRABECULA COMMUNIS
TRABECULA CRANII
QUADRATE
HYPOPHYSEAL FENESTRA
NOTOCHORD
BASICAPSULAR FENESTRA
ROOF OF OTIC CAPSULE
TW

and the ascending processes of the premaxillaries. Articulating with the basal bone at its rostral end, which forms the tip of the snout in this fish, is the skeletal core of the illicial rod. In addition to these 2 supporting parts the illicium includes a small sliver of cartilage borne on the upper surface of the basal bone, just above the point where the latter is supported by the rostral tip of the neurocranium (fig. 2). This small dorsal element is not visible externally but serves for the attachment of 2 pairs of the illicial muscles, as will be described below.

2. Visceral skeleton. The second major specialization of the anterior part of the *Gigantactis* skull is, like the first, due to the unusual development of certain extra-cranial structures. In the foregoing instance this is the presence on the head of dorsal fin rays and in the second case it is the hypertrophy of the second and third branchial arches. Arches 1 and 4 of the 4 present are reduced; epibranchial 1 is incomplete and neither arches 1 nor 4 have upper pharyngeals. In contrast the dorsal elements of arches 2 and 3 are the largest elements present in the branchial skeleton. They are also the only ones strengthened by bone. This runs longitudinally as attenuate splinters (fig. 2).

Uusually dentigerous plates of modest size, the upper pharyngeals of these 2 arches have become huge dorso-ventral pile-like structures from which long sharp teeth depend from the roof of the mouth. The corresponding epibranchials which distally abut on these pharyngeals are strongly developed, too. The remaining parts of the branchial arches are but thin trackers in comparison.

The hypertrophied elements of the branchial skeleton appear even more unusual because of several additional peculiar relationships: the location of the upper pharyngeals far forward of their normal position, the narrowness of the base of the anterior neurocranium, the almost complete absence of circumorbital bones, and the reduced condition of the pterygoid and upper jaw elements. All these allow the relatively enormous pharyngeals to project boldly up into the preocular

region of the face where they are a most peculiar and conspicuous feature (fig. 1). So unusual are they that Regan ('26, p. 12) even mistook them for huge lateral ethmoids in *Gigantactis gracilicauda* (the error was later corrected after a reexamination of this skull, Regan and Trewavas, '32, p. 38).

Between the pharyngobranchials of *Gigantactis longicirra* both the basal and roofing structures of the neurocranium are constricted so that they reach their minimum width at this point, being 50% of the breadth of the vomer and less than 25% of the maximum width of the skull in the mid-otic region. However, the branchial elements and connective tissue fill in the space between the neurocranium and the palatine and pterygoid so that a smooth taper to the external form of the head is maintained, nevertheless, from the eye to the tip of the snout. The relation between the skeletal parts is such that the upper pharyngeals pass dorsally mediad to the palatines but laterad to the frontals.

The size and strong basal support of the otic region of the *Gigantactis* skull correlate not merely with the development of a large inner ear but in addition also reflect the strong lower jaw and hyoid arch. The suspension of these latter structures by the hyomandibular-palatoquadrate series is correspondingly sturdy. In turn the hyomandibular articulates solidly with the otic region by a single head against its ventrolateral margin. The occipital region of the skull is fused to the first vertebra.

In contrast to the lower jaw the upper one has weakly developed skeletal support. The palatine, maxillary and premaxillary (only the last bears teeth) are mere splinters. However, these 3 bones running parallel probably combine to form a functional jaw of moderate strength. There is an ascending process on the premaxillary but it presumably functions in supporting part of the illicium rather than in providing a means of protruding the rim of the upper jaw, as in *Antennarius,* for example.

The opercular elements and the branchiostegals which develop with them from the embryonic opercular flap are mainly

weak ray-like structures. The preopercular and interopercular are reduced to scale-like plates on the surface of other bones of the hyomandibular series. The opercular consists of 2 slim trabeculae which articulate at their junction with the hyomandibular. The longer and more ventral of the 2 bears the subopercular distally as a slender wavy rod paralleling the last of the branchiostegals, which are also thin and drawn out. These elongate trackers of bone all support the membranous covering for the much enlarged branchial cavity, which extends posteriorly over the pectoral girdle in a narrowing tunnel that opens by a sizable vertical slit below the axilla. Such a secondary gill opening, rather than the usual teleost opercular cleft, characterizes pediculates in general.

3. Pectoral girdle and fin. The dermal bones of the pectoral girdle are also attenuate, and the structural relations of cleithrum, supracleithrum and postemporal suggest a mechanism not subject to much stress or strain (fig. 1). The primary girdle, purely cartilaginous, is quite heavily developed with a large coracoid bearing pronounced anterior and posterior processes. The scapula is less massive, and its foramen lies between the 2 primary cartilages. There are 5 proximal radial bones in the *G. longicirra* pelvic fin; this is 1 more than is known in any other ceratioid. Embryological evidence suggests that this is the basic number of these elements for teleosts (Derjugin, '10), but the present case actually represents a secondary increase in number from the 3 which are primitive for the pediculates (Gregory and Conrad, '36).

As usual in deep-sea anglers, the uppermost of these radials is a separate element while the distal ends of the others are fused together in a common plate of cartilage which articulates with all of the fin rays except possibly the most dorsal one. Only the 2 outer radials of these 4 partly fused skeletal units articulate with the primary girdle; the inner 2 are weaker and too short to reach the joint. A pad of connective tissue provides an articulating surface between the base of the radialia and the girdle. This lies largely in the coracoid re-

gion; only about 25% of the articulation of the pectoral is with the scapula. This differs considerably from *Lophius* where the joint is entirely with the scapula (Starks, '30). But in that case the primary girdle elements are smaller and the articulating surfaces more restricted in size. Distal radials were not observed between the proximal radials and the fin rays, although another pad of connective tissue interposes between the outer end of the fused radials and the dermal rays. It should be pointed out that the articulation in *Gigantactis* resembles more a simple hinge rather than the rotating, sliding joint in a functionally pediculate fin like that of *Histrio* or *Antennarius*.

C. Musculature

Like the skeletal elements many of the muscles in *Gigantactis* are reduced in size, and some commonly present in the less highly specialized actinopterygians are lacking altogether. However, certain of these contractile structures have moderate proportions and a few are especially well developed. The Hyohyoideus superior, for example, is reduced to a few scattered strands traversing the branchiostegals, and the cucullaris consists largely of a tendinous band meagerly supplied with muscle fibers in its middle portion (fig. 1). In the category of moderately developed muscles the abductors of the pectoral and the Adductor mandibulae should be mentioned. Their effective functioning gains support from the associated sturdy skeletal parts mentioned above.

The illicium of *Gigantactis* is provided with 5 pairs of muscles (figs. 1 and 9). Posteriorly there are 2 pairs of attenuate muscular slips: retractors and exserters. The former originate from the frontals and insert on the posterior end of the small dorsal element which is firmly bound by connective tissue to the basal bone. These retractors are not only very slim muscles but contractile tissue takes up only about one-third of their length from origin to insertion. From these facts it appears that these muscles are not only weak but also

do not contract through as great a distance as their overall length would indicate (Haines, '32). Their contraction draws the dorsal element backward into the illicial trough and with it the basal bone, thus retracting the articulation of the illicium. The exserters are somewhat stouter and do not have obvious tendons. They originate mesially from the cartilage in the mesethmoid region and course posteriorly and dorsad to insert near the dorsal mid-line of the caudal end of the basal bone. Their contraction pushes the basal bone forward out of the illicial trough.

Anteriorly there are 3 pairs of considerably more powerful muscles. Two of these flex and extend the illicial ray on the basal bone. They originate posteriorly on the latter skeletal element over a broad area so that they cover about four-fifths of it with a sheet of muscle which divides rostrad into extensor and flexor elements. The third pair of anterior muscles are the inclinators of the illicium. Each originates from the lateral ethmoid region just anterior to the origin of the Adductor arcus palatini, runs dorsally over the outer surface of the prefrontal and meets the other member of the pair by inserting on the mid-dorsal line of the small dorsal element. Contraction of the inclinator deflects the distal end of the basal bone laterally and at the same time rolls it over, thus altering the plane through which the illicial rod is flexed and hence the region through which the esca moves. This coupled with the effects of asymmetrical contraction of the flexors and extensors on the 2 sides would give a wide range of movement to the external parts of this organ. The flexor and extensor of the illicium and the inclinator of this structure considerably surpass in size their apparent serial homologs on the other rays of the dorsal fin. In contrast, the exsertor and retractor of the basal bone are elongate but weak.

The largest and most complex muscle system (except the reduced lateral musculature) in this angler is the one which activates the hypertrophied upper pharyngeals and epibranchials of the second and third branchial arches (figs. 1

and 8). In particular the retractor of the branchial arches is enormous, originating broadly on the first 3 and part of the fourth vertebrae and inserting on the pharyngobranchials below their articulations with the epibranchials. Levatores arcuum branchialium externi, 2 and 3, Transversus dorsalis anterior, and Interarcualis dorsalis 2 are also well developed.

Note, however, that the number of branchial muscles present is unusually small. *Gigantactis* has only 3 or 4 Levatores arcuum branchialium present on a side (1 or 2 internal and 2 external) while *Opsanus* (Pankratz, '28) has 5 and *Amia* (Allis, 1897, p. 668), many cypriniform fishes (Takahasi, '25) and *Scomber* (Allis, '03) have 6 or 7. In addition the present form has just the anterior Transversus dorsalis and the superior Retractor arcuum branchialium. Three Obliqui dorsales superior are present. Ventrally the branchial musculature is even further reduced; an Obliquus ventralis on the third or fourth arch was the only muscle observed (not shown in figures).

Furthermore, the presence of a strong ligament ventrally binding the pharyngobranchials together near the base of their teeth and the double insertion of the various muscles on these skeletal parts shows that they are a single functional unit on each side. This reduces the apparent number of independent muscles of the branchial arches to even fewer than they are. Thus Interarcuales dorsales 3 and 4 and Levatores arcuum branchialium interni 2 and 3 are more or less completely fused to single muscle masses and the large Levatores arcuum branchialium externi (2 and 3) have a common origin on the surface of the parietal, although they separate distally to insert on epibranchials 2 and 3 respectively. Just mediad to the external levators, lying between them and the neurocranium is a large mass of connective tissue over the surface of which these muscles lie. The operation of this whole structure as a specialization for bolting food is discussed below.

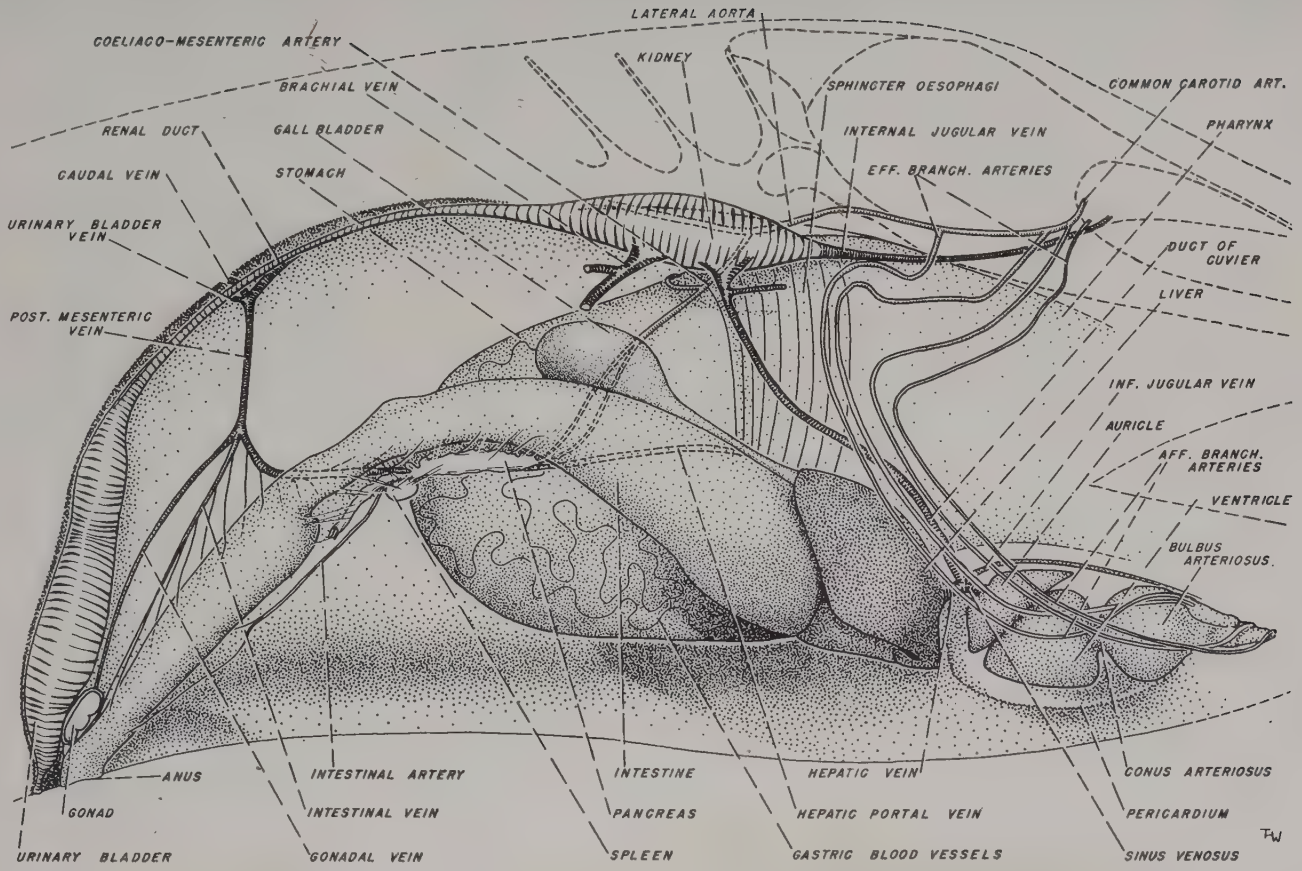
D. Digestive system

The dentition of *Gigantactis* is that of a predator which uses its teeth mainly for the seizing and quieting (by stabbing) of large prey. Like the jaw teeth of *Lophius* (Kampschulte, '39), those present on the dentary and premaxillary have ligamentous attachments which permit them to be depressed inwards or backwards, but not outwards when fully erect, an arrangement that would facilitate the swallowing of food impaled on saber-like teeth of this sort. Maxillaries, palatines, vomer and lower pharyngeals are toothless. The long stabbing teeth on the upper pharyngeal bones have been mentioned but a discussion of their peculiarities will be deferred to later sections where the mechanism of their specialization and operation will be analyzed in detail.

The large pharynx opens abruptly into a blind-ending sac-like stomach (fig. 4), although a weak Sphincter oesophagi between the two is represented by loose bands of constrictor muscle fibers. In its present condition the stomach of this specimen is small but there are indications that, like that of many other deep-sea fish, it is capable of marked distension to accommodate large or numerous prey. First, the coelom is large and would permit considerable expansion of the digestive tract before the elasticity of the body wall would be called upon. Secondly, the blood vessels on the surface of the stomach are embedded in a layer of loose connective tissue and their course is highly tortuous. This could allow excessive stretching of the stomach without causing gastric hemorrhage.

The intestine originates on the right antero-ventral surface of the stomach and no pyloric caeca are present. The general relationships resemble those found in *Lophius* except that 2 caeca are present in the latter (Oppel, 1896, pp. 86–87). The small intestine of *Gigantactis* is narrow and tapers posteriorly. Arching dorsally it joins the large intestine, which like

Fig. 4 Lateral view of viscera of *Gigantactis*. × 10. Note that for clarity the branchial arteries have been drawn as though they were continuous rather than interrupted on the gill arches, as they are, by the capillary circulation of the gill filaments.


LATERAL AORTA
COELIACO-MESENTERIC ARTERY
KIDNEY
BRACHIAL VEIN
SPHINCTER OESOPHAGI
COMMON CAROTID ART.
RENAL DUCT
GALL BLADDER
INTERNAL JUGULAR VEIN
PHARYNX
CAUDAL VEIN
STOMACH
EFF. BRANCH. ARTERIES
URINARY BLADDER VEIN
DUCT OF CUVIER
LIVER
POST. MESENTERIC VEIN
INF. JUGULAR VEIN
AURICLE
AFF. BRANCH. ARTERIES
VENTRICLE
BULBUS ARTERIOSUS.
ANUS
INTESTINAL ARTERY
INTESTINE
HEPATIC VEIN
CONUS ARTERIOSUS
GONAD
INTESTINAL VEIN
PANCREAS
HEPATIC PORTAL VEIN
PERICARDIUM
URINARY BLADDER
GONADAL VEIN
SPLEEN
GASTRIC BLOOD VESSELS
SINUS VENOSUS
TW

whether all these afferent renal veins are truly parts of the portal system of the kidney. However, such vessels in other actinopterygians have been found to break up and anastomose in the tissue of the kidney before flowing into the renal vein (Allen, '05). From the kidney the duct of Cuvier runs ventrally (and antero-medially) to the sinus venosus by an attenuated course. The only parts of the venous returning to the heart which do not come through the kidney are the contributions of the hepatic veins, the inferior jugular, and a small vein which enters the duct of Cuvier from the esophageal region (fig. 4).

F. Excretory system and gonads

The kidneys lie far forward beside the first 3 vertebrae and the occipital region of the skull (fig. 4). No arterial supply to this organ was observed, but this is consonant with previous findings in the neritic pediculate, *Lophius,* that it is reduced (Marshall and Grafflin, '28) or absent (Audigé, '10). The relations of the kidneys to the veins has been described above. No microscopic examination has been made of the *Gigantactis* kidney so that the nature of its functional elements is unknown. However, in those pediculates which have been studied (Marshall, '27; Grafflin, '29) nonfunctional or absent glomeruli indicate that this group also reflects the widespread tendency of marine *Osteichthyes* to reduce the filter bed of their kidneys (Owen, '38; Smith, '43).

Posteriorly the nephric ducts lead to a large urinary bladder which opens to the exterior by a pore just behind the anus. Between the distal end of the bladder and the rectal portion of the large intestine are the small gonads. The genital pore which in teleosts normally opens between the anus and the excretory papilla was not observed, but it is undoubtedly weakly developed in an individual such as this, whose sex organs suggest its immaturity. Since the gonads were not sectioned, the sex of the specimen was not determined. However, all previously studied specimens in the family are fe-

males and no gigantactinid male is definitely known (Regan and Trewavas, '32).

G. Nervous system and sense organs

1. Brain. The most striking feature of the brain of *Gigantactis* is the weak development and peculiar position of its parts anterior to the medulla oblongata (fig. 5). The forebrain, while not particularly notable for its size, is displaced as if it had been compressed backward and downward from its normal position. The mesencephalon and metencephalon are correspondingly telescoped. The result of these changed relations is that the anterior end of the forebrain, instead of occurring at a level well above the axis of the brain and cord, and far anterior to the hypophysis as would be expected of most teleosts (Herrick, 1899; Cole and Johnston, '01; Pankratz, '30), is found somewhat below and in the same transverse plane as the trigemino-facialis ganglionic complex. In *Opsanus* [phylogenetically close to the pediculate type (Gregory, '33, p. 382 and plate II)], the latter occurs just lateral to the optic tectum (Pankratz, '30). Thus the anterior crista of the semicircular canals in *Gigantactis* lies slightly ahead of the tip of the forebrain instead of lateral to the region between the mesencephalon and the metencephalon which is considerably behind this point. Furthermore, the adenohypophysis, instead of projecting ventrally from between the lateral lobes of the mesencephalon, lies entirely anterior to the forebrain and is connected with the infundibulum by a long tenuous stalk, which has a curious knob-like swelling halfway along its length.

The optic lobes of the *Gigantactis* brain are small in size. Also weakly developed is the cerebellum. It is visible externally as a slight bulge, which is peculiar in being divided anteriorly into 2 lobes by a groove in the mid-line.

As the site of origin of the only well developed cranial nerves (V, VII, VIII, IX, X), the medulla oblongata is appropriately enough the largest by a considerable margin of

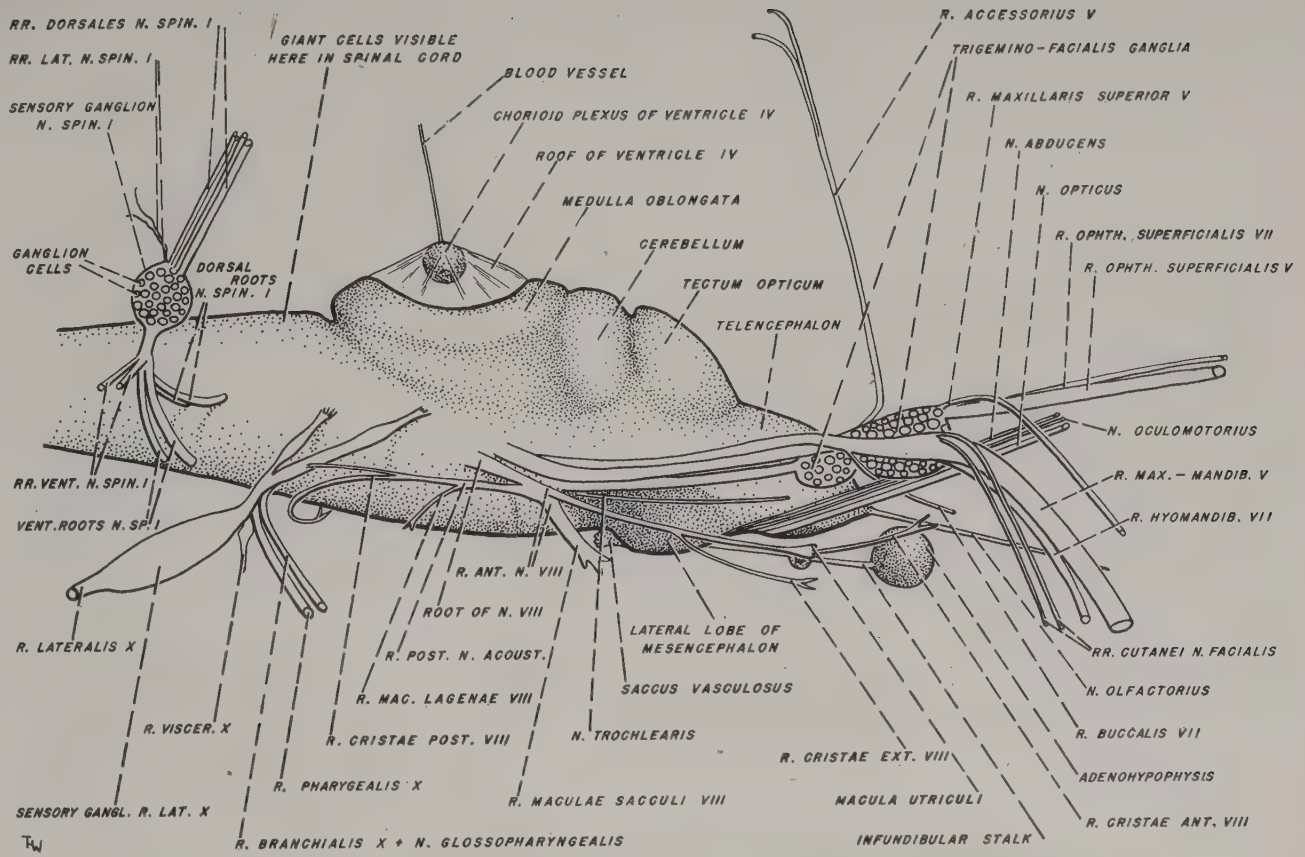
the 4 main parts in the brain stem of this fish. It is about half the length of the whole brain and the widest and deepest points in the central nervous system occur in the anterior portion of this region. A peculiar horseshoe-shaped swelling marks the anterodorsal limits of the nervous part of the medulla.

Because the cerebellum is so weakly developed, the whole roof of the medulla oblongata is visible. It consists largely of non-nervous, transparent epithelium. Just within this paper-thin layer a spherical knot of tissue, somewhat smaller than the hypophysis, is suspended by a small intracranial blood vessel (fig. 5). From its gross appearance and relations, this structure is presumably the chorioid plexus of the fourth ventricle, but histological study would be required to confirm this.

2. Cranial nerves. The most striking feature of the cranial nerves as a whole is the relatively strong development of nerves consisting predominantly of acoustico-lateralis and somatic sensory elements. Certain of the motor efferents are moderately developed but a considerable portion of this part of the peripheral nervous system is much reduced. Thus, the trigemino-facialis ganglia have as great or greater volume than the optic tecta, the Ramus lateralis vagi is large, and the eighth nerve (particularly the R. maculae sacculi) is well developed; on the other hand cranial nerves I, II, III, IV, VI, IX are quite attenuate (fig. 5).

The general topology of these peripheral nerves shows considerable influence of skull peculiarities and the particular arrangement of the corresponding effector and receptor organs. For example, the olfactory tract and other innervation of the snout are notably attenuated by the elongation of the

Fig. 5 Brain and anterior end of spinal cord of *Gigantactis*. Lateral view × 34. Note that all brain elements anterior to the medulla oblongata are relatively small and have been compressed downward and backward from their typical teleost relationships. The possible dependence of this peculiarity on the morphogenetic effects of the illicium is discussed in the text (p. 138).


RR. DORSALES N. SPIN. I
RR. LAT. N. SPIN. I
SENSORY GANGLION N. SPIN. I
GANGLION CELLS
DORSAL ROOTS N. SPIN. I
GIANT CELLS VISIBLE HERE IN SPINAL CORD
BLOOD VESSEL
CHORIOID PLEXUS OF VENTRICLE IV
ROOF OF VENTRICLE IV
MEDULLA OBLONGATA
CEREBELLUM
TECTUM OPTICUM
TELENCEPHALON
R. ACCESSORIUS V
TRIGEMINO-FACIALIS GANGLIA
R. MAXILLARIS SUPERIOR V
N. ABDUCENS
N. OPTICUS
R. OPHTH. SUPERFICIALIS VII
R. OPHTH. SUPERFICIALIS V
N. OCULOMOTORIUS
R. MAX.-MANDIB. V
R. HYOMANDIB. VII
RR. VENT. N. SPIN. I
VENT. ROOTS N. SP. I
R. ANT. N. VIII
ROOT OF N. VIII
LATERAL LOBE OF MESENCEPHALON
R. LATERALIS X
R. POST. N. ACOUST.
SACCUS VASCULOSUS
RR. CUTANEI N. FACIALIS
N. OLFACTORIUS
R. MAC. LAGENAE VIII
R. VISCER. X
R. CRISTAE POST. VIII
N. TROCHLEARIS
R. BUCCALIS VII
R. CRISTAE EXT. VIII
ADENOHYPOPHYSIS
R. PHARYGEALIS X
R. MACULAE SACCULI VIII
MACULA UTRICULI
R. CRISTAE ANT. VIII
SENSORY GANGL. R. LAT. X
R. BRANCHIALIS X + N. GLOSSOPHARYNGEALIS
INFUNDIBULAR STALK
TW

preoptic region of the skull and the telescoping of the anterior parts of the brain. As a result of this latter peculiarity and the large size of the otic labyrinth, the roots of all the cranial nerves anterior to IX and X are stretched out and incline forward at an acute angle to the brain's axis. The optic nerve consequently is about equal in length to the brain, and as mentioned above, the ganglia of the trigemino-facialis complex are at the level of the anterior end of the forebrain (fig. 5).

Perhaps the most noteworthy individual cranial nerve component is a large branch which innervates the illicium on either side (figs. 1, 5, and 9). This nerve is obviously a part of the superior optic trunk which supplies mainly the lateral line and general cutaneous receptors in the upper region of the orbit and the dorsal surface of the snout (Herrick, '00; Allis, '03; Pankratz, '30). This trunk is typically made up of closely associated Rami ophthalmici superficiales from the fifth and seventh cranial nerves. One of these is much larger than the other in *Gigantactis longicirra* and runs to the illicium. In the absence of direct neurological evidence this can be identified only inferentially since the trigemino-facialis complex was not unsnarled by the dissection.

Two lines of evidence show that this illicial nerve is the one usually referred to in teleosts as the R. superficialis ophthalmicus trigeminus. First is the fact that unlike the typical superficial ophthalmic VII, which carries only lateralis fibers, the illicial nerve gives off no branches until it reaches the region of the snout just below the tubular nostril. Also, the esca of *G. vanhoeffeni,* although it was found to contain sensory endings in epithelial papillae, gave no indication of having any lateral line type of end organs present (Brauer, '08). Second, the other component of the superior optic trunk of *G. longicirra,* which terminates in the skin on the side of the snout, does give off several branches to the skin in the region of lateral line organs. Hence the latter is concluded to be a facialis component and the illicial nerve of cranial origin to be the trigeminal element.

The R. superficialis ophthalmicus V runs anteriorly in company with the corresponding facialis ramus to the level of the upper pharyngeals, where it takes a deeper course than the latter, passing beneath the inclinator of the illicium and the prefrontal (fig. 9). A small part of the nerve in question ramifies over the dorso-lateral surface of the vomer, and innervates the skin below and lateral to the nostril. The major portion of the ramus continues on to the lateral surface of the illicium out which it runs to the esca.

This large cranial nerve branch supplying the illicium has not been described before. Brauer ('08) prepared serial sections of the head of *G. vanhoeffeni* from which he made a reconstruction, but he failed to find any cranial innervation of the fishing filament. From a morphogenetic and phylogenetic point of view the present discovery is of considerable interest since it definitely represents a secondarily acquired innervation for a part of the dorsal fin. If the cranial illicial nerve is similar to the so-called Superior ophthalmicus V in other teleosts, it carries general cutaneous sensory fibers of trigeminal origin and in addition some visceral sensory neurons, which stem from gustatory elements of the facialis (Herrick, '01, pp. 202–203).

It should be noted here that the peculiar anastomosis observed between R. crista posterioris VIII and the root of IX-X has not been reported before (fig. 5). It would be necessary to identify the fibers it carries before its function is understood.

The roots of the glossopharyngeal and vagus nerves are reduced, there being only 2 between them (fig. 5). Without a study of the fibers involved it is impossible to tell whether the anterior of these is the lateralis root of X plus the root of IX or merely the latter. In view of the definitely limited peripheral distribution of the glossopharyngeal to the first branchial arch, which is much reduced in this fish, the former of these alternatives seems more likely. In either case the 2 roots merge just inside the skull so that a single trunk issues

from the foramen. This immediately branches into 6 rami of quite different diameters (fig. 8).

The most anterior of these is of medium size and turns cephalad beneath the hyomandibular. This ramus has several ganglionic masses present in its distal ramifications. It divides into 5 main branches which are distributed to the branchial arches. From work on other teleosts (e.g., Cole and Johnstone, '01; Allis, '03), one would expect that the twig innervating the first hemibranch and the still more anterior ramulus comprise the glossopharyngeal elements; the other 3 branches then are vagus components. It was not possible to work out all the details of the innervation of the branchial arches. However, a large motor ramus divides to innervate the branchial muscles, while various other ramuli, including sensory components (as indicated by the extracranial ganglia) are distributed to the other elements (fig. 8).

The next ramus issuing from the vagus foramen is about equal in size to the first but shows no gross evidence of containing afferent neurons; it provides the motor innervation for the enormously developed retractor of the branchial arches.

Posterior to this is an extremely thin ramus which innervates the cucullaris muscle: the R. accessorius "XI." Next comes a large ramus with a sensory ganglion on its course; this provides the visceral innervation of the vagus, dividing at once into an anterior branch which carries fibers of the R. cardiacus X and R. oesophageus X and a posterior R. intestinalis X. Just behind this is an extremely tenuous R. cutaneus dorsalis X which sends fine branches to the skin of the "shoulder" region.[3]

Last is the largest branch of the vagus, the Ramus lateralis X which swells into an elongate ganglion as soon as it splits off from the main trunk. Passing caudad this ramus divides shortly into a number of ramuli which supply the lateral line organs of the whole postcranial region of the fish. No lateralis

[3] Neither this ramus nor the R. accessorius are shown in the figures.

ramulus has been displaced into an unusual position by the cephalic position of the anterior parts of the dorsal fin. This is in contrast to the situation in the shark sucker, *Echeneis*, where the modification of the anterior dorsal into a cephalic sucking disc has brought not only spinal nerves onto the skull but also a large branch of R. lateralis X (Houy, '10). But in this latter fish, the cephalad movement of the dorsal fin has provided a much more extensive replacement of the normal dorsal surface of the head than has the illicium of *Gigantactis*. Hence a more drastic reorganization of the lateral line organs of this region would be necessary in the shark-sucker.

The points of particular interest about the ninth and tenth cranial nerves are: first, the dominance (again) of the lateralis components of the system; second, the relatively high importance of the visceral efferent fibers to the muscles of the dorsal part of the branchial arches.

3. Sense organs. a. Olfactory. The nostrils of *Gigantactis* are slender, tubular structures just lateral to the base of the illicium in the prefrontal region. What appeared on dissection to be the sensory surface is small in size and uncomplicated. The cranial nerve supplying these organs is slender and long drawn out by the lengthening of the preoptic region of the head. Neither the sense organ nor its innervation would suggest that olfaction provides a major afferent barrage to the *Gigantactis* brain.

b. Optic. The eye of *Gigantactis* is small; in the present specimen its diameter is only 1/50 of the standard length of the body. According to Brauer ('08) the eye of *G. vanhoeffeni* shows histological evidence of marked regression, but this has not proceeded to a state where the organ may be properly considered vestigial.

In *G. longicirra* the complete absence of a functional skeletal orbit (fig. 2) and the hypertrophy of dorsal muscles of the branchial arches leaves the eye, freely suspended by its optic nerve and 4 rectus muscles (fig. 1). These all emerge from the skull at about the level of the hypophysis and their course continues sharply forward and somewhat dorsal as they run

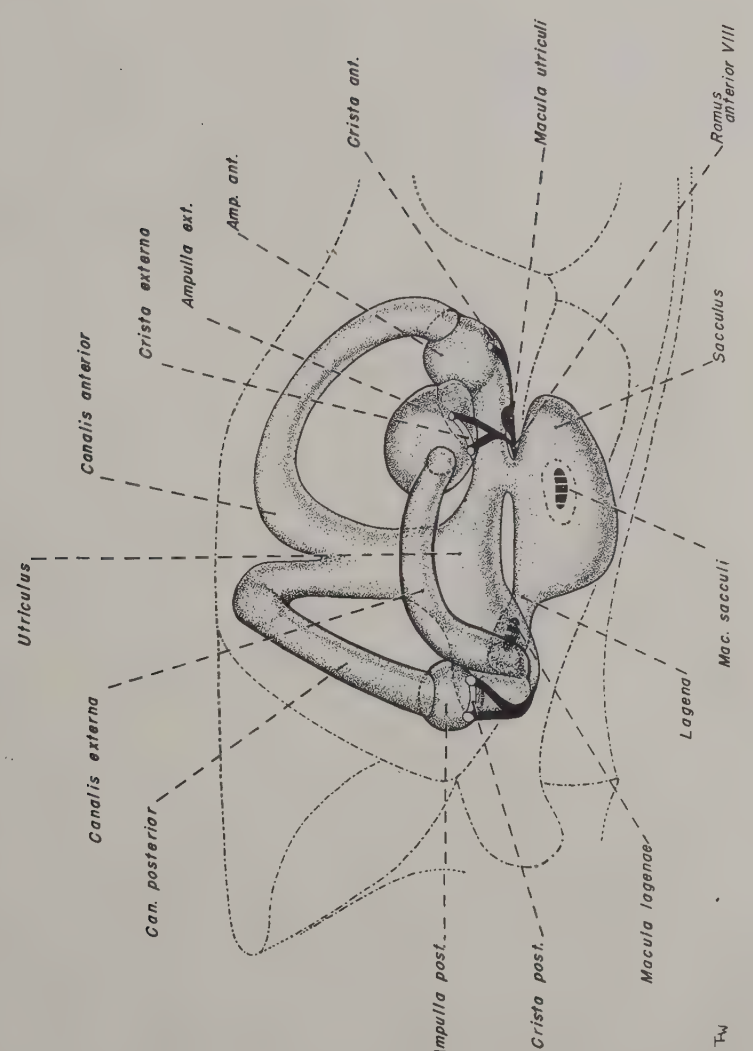
up and over parts of the internal and external levators of the branchial arches then downward to the eye itself, which rests against the outer surface of the Obliquus dorsalis superior externus (probably the Obl. dors. sup. 2 with its insertion shifted to the outer surface of the second pharyngobranchial).

The oblique muscles of the eye have normal insertion and even normal origin in the region of the nasal septum. But the fact that this site of the anterior myodome has been carried far forward by the elongation of the preoptic region of the skull stretches these oblique muscles to an exceptional degree (fig. 1). They are about as long as the generous gape of the fish!

Lying free as it does, the eye presumably would be capable of extensive movement; yet the eye muscles and their motor nerves are tenuous and appear quite unlikely to provide accurately controlled vigorous eye movement such as occurs in fish which live in the well illuminated regions of the sea and use vision as an important sense in pursuing prey. In addition the eye lies within the surface of the body and must peer at the outside world through a small oval hole in the otherwise heavily pigmented skin (Waterman, '39b, fig. 1).

c. Stato-acoustic. The labyrinth of *Gigantactis longicirra* (fig. 6) is large relative to the size of the skull despite the latter's elongate preoptic region; it is even larger when considered in relation to the brain and eye. In spite of the basic conservatism of the labyrinth (especially the dorsal part of it) throughout the gnathostome vertebrates (de Burlet, '34), that of *Gigantactis* shows certain modifications in detail. Such modifications are quite varied in teleosts and produce a series of inner ear types which are characteristic of different bony fish groups (Froese, '38, p. 636). As in other *Pediculati* (Bierbaum, '14) the Canalis sacculi-utriculi and the Macula

Fig. 6 Lateral view of the inner ear of *Gigantactis*. × 24. Noteworthy are the relatively huge size of the whole labyrinth, its well developed innervation and sense organs, and the large sacculus and lagena. Despite widespread deformation of other cranial structures around it, the basic plan of this organ is strikingly conservative.


Utriculus
Canalis anterior
Cristo externo
Ampulla ext.
Amp. ant.
Crista ant.
Macula utriculi
Ramus anterior VIII
Sacculus
Canalis externa
Can. posterior
Ampulla post.
Crista post.
Macula lagenae
Lagena
Mac. sacculi

neglecta are absent. The semicircular canals are well developed and their ampullae large, especially that of the horizontal canal. Lagena and sacculus are present but the Ductus endolymphaticus was not observed. This duct was described (Bierbaum, '14) in *Dolopichthys,* another deep-sea angler-fish, whose inner ear otherwise is very similar to that of *Gigantactis* in proportion, size, and position relative to the brain.

The eighth cranial nerve and the cristae and maculae which are its sensory end-organs, are well developed. They suggest that the sensory data provided by the inner ear are important in the behavior of this angler-fish. The cupulae of the cristae and the otoliths of the maculae were not observed; the latter had undoubtedly been dissolved by the original fixation of the specimen.

4. Spinal cord. From the posterior end of the myelencephalon the spinal cord of *Gigantactis* tapers rapidly and at the level of the third or fourth vertebra has been altered to a Cauda equina consisting of a Filum terminale accompanied by a dorsal bundle of sensory roots and a somewhat larger ventral bundle of motor roots. Such an anterior origin for the roots of the spinal nerves has been observed in a number of teleosts; it is particularly marked in *Orthagoriscus* (Burr, '28) and *Lophius* (Ariëns Kappers, Huber and Crosby, '36, fig. 79).

At its forward end where it gives rise to the large first cervical nerve, the spinal cord is scarcely smaller than the medulla (fig. 5), but it does not have any obvious enlargements or swellings such as are associated with hypertrophied sensory roots in *Lophius* (Ariëns Kappers, '06) or *Trigla* (Herrick, '07). However, giant cell bodies can be seen in the dorsal region of the medulla as it emerges from the skull. These were first discovered in *Lophius* (Fritsch, 1886) and since found to occur in many teleosts (e.g. Sargent, 1898; Tagliani, 1899). They are the cell bodies of a type of sensory neuron whose perikaryon is intradural or intramedullary in position. Such neurons are not found in plagiostomes but do occur in

cyclostomes. Their function is unknown but believed to be a primitive one.

The spinal cord and Cauda equina are enclosed by a transparent tubular layer of the Meninx primitiva (dural layer) (fig. 10). This is separated from the cord by a considerable space, which is presumably filled in part by leptomeningeal tissue if the structure of the meninx parallels that of *Lophius* (Ariëns Kappers, '25).

5. Spinal nerves. The first spinal nerve is one of the most interesting components of the anatomy of *Gigantactis*. Not only does it contribute to the brachial plexus, but it also provides motor and sensory fibers to the illicium. As soon as it emerges from its foramen between the first vertebra and the occiput the first spinal nerve divides into 2 ventro-lateral rami and a large dorsal trunk (fig. 5). Each of the former swells into an elongate ganglion soon after its origin and then continues on to the pectoral girdle where it forms one of the 4 large nerves on either side innervating this structure (fig. 7). The anterior of the 2 ventro-lateral rami gives rise to a R. cervicalis.

The dorsal trunk of the first spinal nerve expands into a spherical ganglion close to its origin. Thence it takes an extraordinary course dorsally and anteriorly over the occipital and supraoccipital regions of the skull.[4] As it passes along the side of the basal bone of the illicium, this nerve branches at the level of the eye for the first time (fig. 9). Here it gives off ramuli for the exserters, retractors, extensors, and flexors.

A large branch continues forward supplying 2 small twigs to the inclinator. The major part of the ramus finally runs under the latter muscle out on the illicial rod to the esca. Peripherally the spinal illicial nerve joins company with a nerve of cranial origin which carries trigeminal fibers to the snout. This superior ophthalmic V does not innervate any part of the basal bone and runs onto the illicium in the rostral

[4] Such a spinal innervation of the muscles in the angling apparatus of *Lophius* has been known for a long time (e.g., Bailly, 1824).

region to accompany the first spinal out onto the esca. The terminal distribution of these very large nerves was not determined as histological study of the esca, an important specific character of this holotype, would have been necessary.

All the components of the first spinal nerve indicate that it is double in origin. There are 4 roots, 2 dorsal and 2 ventral; the illicial nerve consists of 2 pairs of elements. The 2 larger of these are the Rami dorsales, the 2 smaller are probably the Rami communicantes of the usual spinal nerve. The ventrolateral components are likewise double.

The second and third spinal nerves are single, each with 1 sensory and 1 motor root. The lateral and ventral rami, like those of the first spinal, innervate the pectoral fin and girdle. The 2 more superior rami are inconspicuous and presumably are the Rr. dorsales and communicantes. The sensory ganglia of these strictly spinal nerves are near the spinal cord and, unlike those of the first cervical which differs by being "spino-occipital" in emergence, are not external to the origins of the Retractores arcuum branchialium.

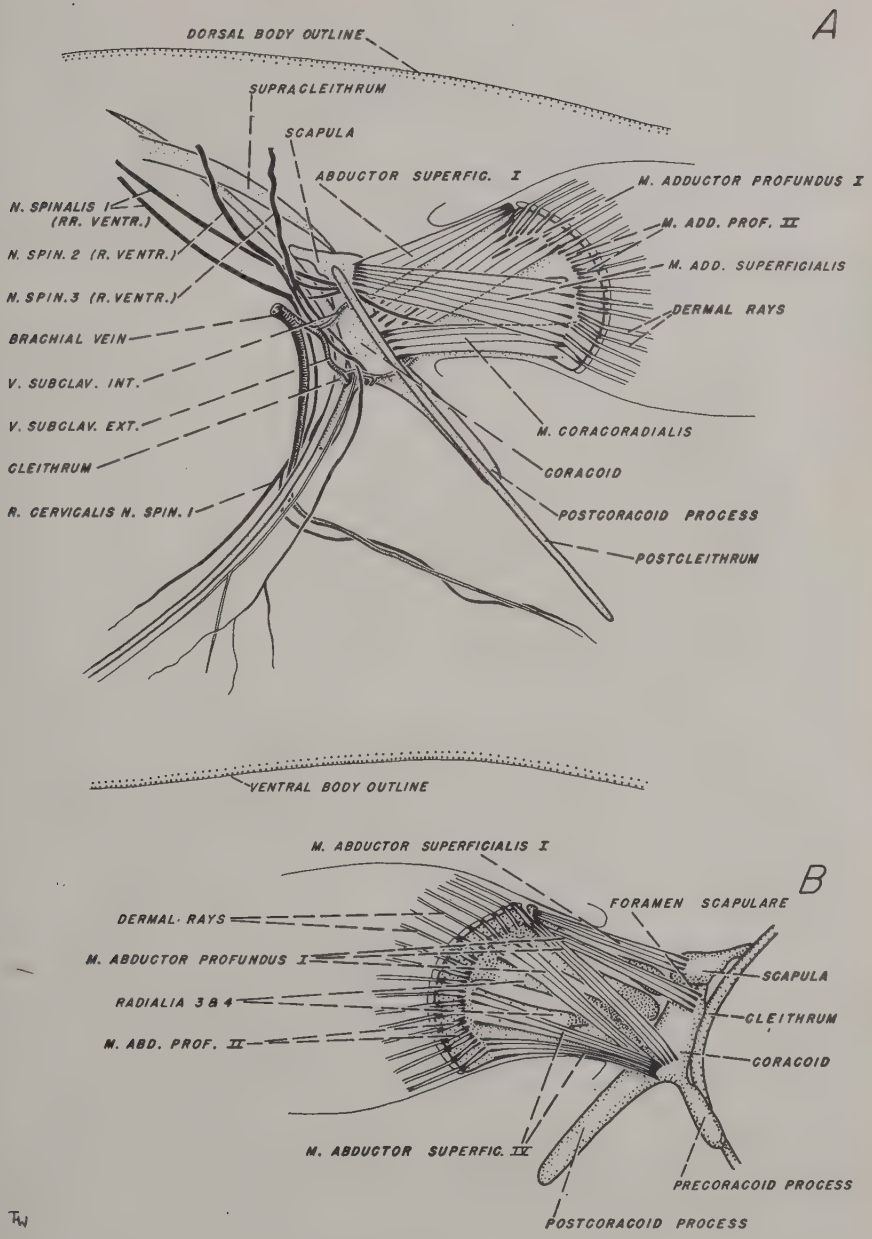
Spinal nerves further posterior are characterized by very elongate roots which form part of the Cauda equina (fig. 10). The sensory ganglia are so placed that they bridge their dorsal and ventral roots. These ganglia have 15–18 cell bodies of various sizes visible within them. Each spinal nerve branches into 4 rami (fig. 10) as is typical for teleostomes.

Fig. 7 The pectoral fin and girdle of *Gigantactis*.

A. Mesial view of right pectoral fin and associated structures. × 10. Note that the ventral rami of the first spinal nerve have apparently been towed caudad by the posterior displacement of the pectoral girdle effected through the enlargement of the pharyngo-branchial cavity.

B. Lateral view of right pectoral fin and girdle. × 10. Mm. abductores superficiales II and III, which are shown in figure 1, have been dissected away to show the underlying elements.

Observe that the articulation of the fin is more hinge-like than it is in a highly developed pediculate structure like that found in *Lophius* or *Antennarius*. Also that the abductor muscles are considerably larger than the adductors which is not the case in teleosts where the pectoral fin is an important propulsive agent in forward locomotion. Muscle terminology follows that of Grenholm ('23) for other pediculates.


A
DORSAL BODY OUTLINE
SUPRACLEITHRUM
SCAPULA
ABDUCTOR SUPERFIC. I
M. ADDUCTOR PROFUNDUS I
M. ADD. PROF. II
M. ADD. SUPERFICIALIS
DERMAL RAYS
N. SPINALIS I (RR. VENTR.)
N. SPIN. 2 (R. VENTR.)
N. SPIN. 3 (R. VENTR.)
BRACHIAL VEIN
V. SUBCLAV. INT.
V. SUBCLAV. EXT.
CLEITHRUM
R. CERVICALIS N. SPIN. I
M. CORACORADIALIS
CORACOID
POSTCORACOID PROCESS
POSTCLEITHRUM
VENTRAL BODY OUTLINE
M. ABDUCTOR SUPERFICIALIS I
B
FORAMEN SCAPULARE
DERMAL RAYS
M. ABDUCTOR PROFUNDUS I
RADIALIA 3 & 4
M. ABD. PROF. II
SCAPULA
CLEITHRUM
CORACOID
M. ABDUCTOR SUPERFIC. IV
PRECORACOID PROCESS
POSTCORACOID PROCESS

It should be pointed out that the motor roots of the spinal nerves are all larger than the corresponding sensory roots, even in the first spinal, although the difference is less marked here. In *Lophius* such a relation is found in the more posterior spinal nerves, but in the cervical ones the sensory roots are considerably the larger, a situation believed to be correlated with a high cutaneous sensitivity over the broad upper surface of this fish's head (Ariëns Kappers, Huber and Crosby, '36, p. 176). This implies that in *Gigantactis,* with the exception, perhaps, of the illicial nerve, general somatic sensory impulses are not particularly developed in the regions innervated by the spinal cord.

IV. ANALYSIS AND DISCUSSION

In the preceding section (III) a considerable number of anatomical facts were mentioned which have morphogenetic and phylogenetic implications of particular interest. These will now be analyzed as integral parts of the functional systems to which they belong.

A. Swimming

Despite its elongate and slim body, there are several lines of evidence which imply that *Gigantactis* is a weak swimmer and that active locomotion does not make up a large part of its behavior pattern. First, the body musculature, which plays the major locomotory role in most good swimmers (von Holst, '39), is weak and not well developed. Then the structure of the fins and their musculature is not that of highly effective propulsive organs. The caudal fin, for example, with its long trailing rays, resembles more the drooping comet tail of certain gold-fish varieties than it does the sturdy falciform tail of wide-ranging active fish like the bonito. Furthermore, the position and anatomy of the pectoral fins indicate that these are not used as paddles for vigorous swimming. When they are important in propulsion, the pectorals in other fish usually lie just ahead of and below the center of gravity of

the body and have the adductor musculature more powerfully developed than that of the abductors (Harris, '37). But in *Gigantactis* the fin lies above the longitudinal axis of the body on which the center of gravity usually occurs; also the pectoral abductors considerably exceed the adductors in size (fig. 7). Finally, the secondary pectoral girdle which must anchor the fin to the rest of the body, is quite attenuate and weakly supported in this fish.

The relatively well developed abducting muscles suggest that braking action or backward swimming is a more effective function of the pectoral fin. However, in most teleosts where braking action to stop forward glide is a major pectoral activity, as it is in the percoids, the pelvic fins have migrated to an anterior position and counteract the lifting force produced by the pectorals (Harris, '38). The complete absence of pelvic fins in known ceratioids and the presence of a reduced pediculate fin, rather than a typical ichthyopterygium, would thus except *Gigantactis* from this familiar swimming type.

Internal evidence for weakly developed locomotor activity may also be found in the brain of this angler-fish: the cerebellum is a relatively inconspicuous structure (fig. 5). Now it has been difficult, physiologically, to establish the function of the cerebellum in fishes since ablation of this part of the brain does not usually result in major dysfunctions. But the findings of comparative anatomy have tended to show a good correlation between degree of development of the roof of the metencephalon and locomotor activity of the teleost concerned (ten Cate, '35). Furthermore, much experimental evidence, mainly embryological, has shown that peripheral receptor and effector fields have a marked effect on the degree of development of their corresponding nerves, ganglia and nuclei (e.g. Piatt, '46). Thus hypertrophy of the central and peripheral nervous elements concerned follows an increase in the sensory or motor load at the periphery; conversely a decrease in this load results in hypotrophy.

From a neurological point of view the cerebellum is a major site of correlation for proprioceptive impulses which

acquaint the organism with its orientation and movement in space. In actively swimming fishes this part of the brain forms an extensive lobe which arches backward over a considerable area of the medulla and may extend forward over the mesencephalon as well (Lissner, '23). In *Gigantactis* no such structure is developed. The much reduced character of the region in this angler fish adds further support to the evidence provided by the muscular system, skeleton and fins that it is a swimmer of strictly limited activity.

B. Feeding

A factor which has, in an adaptive sense, conditioned the morphology of *Gigantactis* to a marked degree is the fish's specialization as a floating trap. The structural details of this adaptation as a voracious feeder result mainly from the greatly enlarged mouth and pharyngeal region with their formidable armature of teeth. Such modifications are not peculiar to this deep-sea angler but are characteristic of most ceratioids and other pediculates as well (Gregory, '33). The tunnel-like prolongation of the branchial cavity caudad to an opening beneath the pectoral fin base and the concomitant attenuation of the branchiostegal and opercular elements is also part of the typical picture (fig. 2). In most *Ceratioidea* this great expansion of the pharyngeal region, as it has in *Gigantactis,* moves the pectoral fins high onto the sides of the body (Gregory and Conrad, '36). It also displaces them posteriorly so that the articulation of the radial bones with the girdle occurs in the present species at the level of the fourth vertebra. In consequence the ventral rami of the first 3 spinal nerves, which innervate the pectoral girdle, are elongated in the same direction (fig. 7). This condition indicates that during development a normal innervation pattern was established before the fin base moved posteriorly and elongation of the nerve rami was produced by "towing" (Weiss, '41, fig. 1).

A similar but more extreme case of the same sort of displacement occurs in teleosts of the Order *Apodes* in which

there is no post-temporal and the pectoral girdle in consequence does not articulate with the skull (Gregory, '33, p. 202). This freedom of the girdle and the enlarged syringe-like branchial cavity combine to move the whole pectoral structure posteriorly. In a deep-sea eel, *Derichthys serpentinus* (330 mm standard length) preliminary dissection by the author showed that this "free floating" fin is displaced caudad until its base lies at the level of the seventh-eighth vertebrae. Nevertheless the fin is still innervated by spinal nerves 1–4, whose fibers it has towed posteriorly to its adult position. Crowded out of the way and not supplying the fin at all are spinal nerves 5–8. A further striking point in *Derichthys* is the fact that the ventral rami of the first 2 or 3 spinal nerves, after supplying the fin, continue ventrally and turn cephalad to run as a Ramus cervicalis to the throat region, terminating at a point even anterior to the level of their original emergence from the axial skeleton.

Although the pharyngeal and pectoral relationships in *Gigantactis* imply morphogenetic processes of considerable interest, they are not as peculiar to this angler as the marked hypertrophy of the dorsal elements of the branchial arches and their musculature. These structures are particularly adapted for powerfully aiding deglutition.

The branchial elements which actually come in contact with the prey are the 6 enormous fang-like upper pharyngeal teeth on either side of the roof of the mouth. The skeletal structures bearing these teeth are much elongated in their original antero-posterior axis (fig. 2). This has been rotated so that it now lies in a dorso-ventral direction. Evidence for this change in orientation is shown in the curiously elongate and sinuous course taken by the Transversus dorsalis anterior which originates in the mid-line of the roof of the mouth and inserts on the pharyngobranchials (fig. 1).

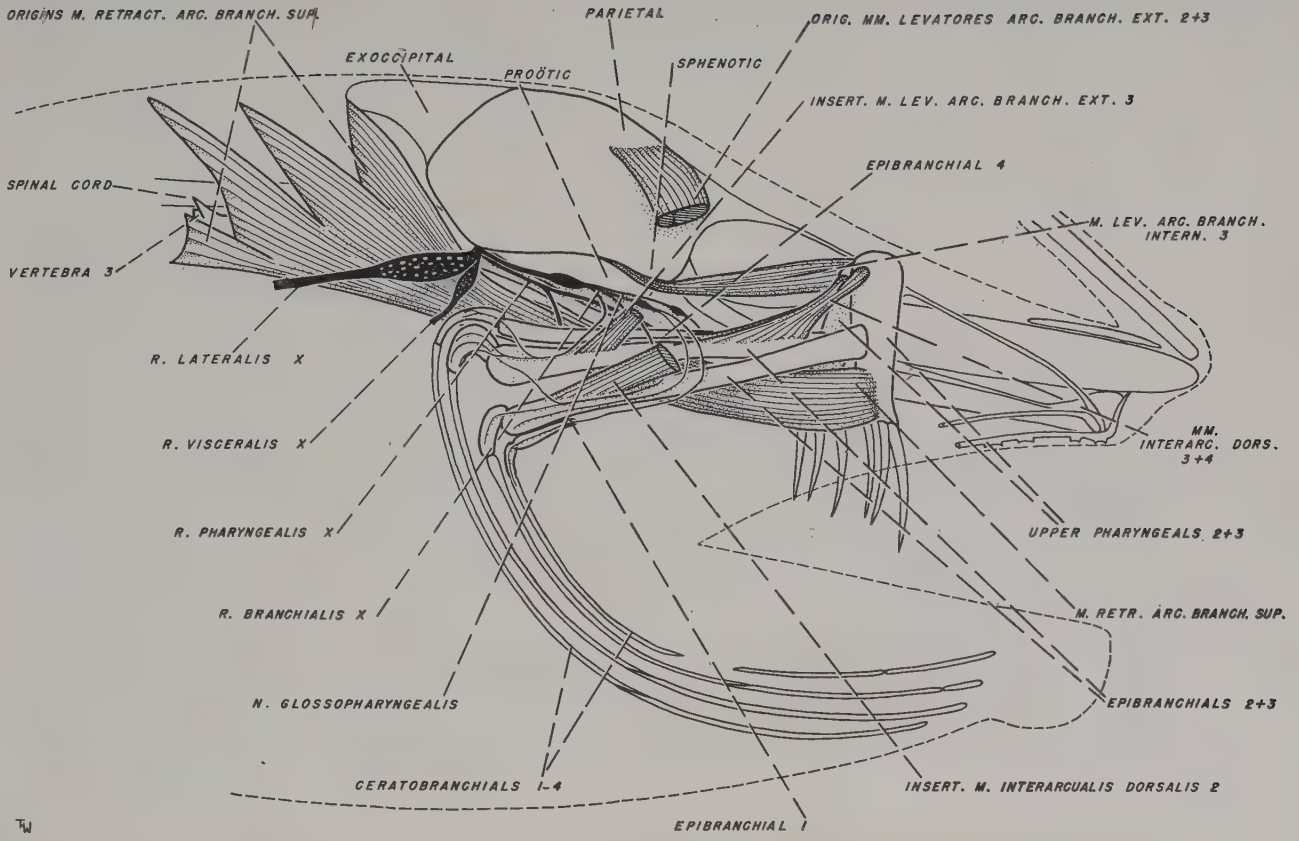
These upper pharyngeals are pivoted midway along their length with the upper ends of the second and third epibranchials (fig. 2). The latter are stout structures elongated so that they thrust the upper pharyngeals distinctly forward of the

optic region where they are in a position to engage prey held by the jaw teeth. In most teleosts the pharyngobranchials lie behind the eye; in *Scomber,* for example, the most anterior lies caudad to the origin of the Adductor hyomandibularis (Allis, '03, p. 133). This apparently is true for the deep-sea angler, *Lasiognathus* (Gregory, '33, fig. 275), although a strong contraction of the Retractores arcuum branchialium on fixation of the specimen could displace the branchial elements from their "resting" position. In *Himantolophus* (Lütkin, 1887) the upper pharyngeals lie somewhat forward of this, just beneath the anterior flange of the proötic. However, their size is moderate and their position still considerably posterior to the preoptic location in *Gigantactis.*

The epibranchials and pharyngobranchials of the second and third gill arches are the largest units of the branchial skeleton. Correlated with this hypertrophy are the large muscles which move these parts on themselves and relative to the rest of the body (fig. 8). Despite this functional specialization, the number of muscles, as mentioned above, is smaller than that found in most teleosts. It is noteworthy that a structural system like the branchial arches, which has undergone a distinct reduction in the complexity and number of its components during the evolution of the higher fishes, should become particularly specialized in *Gigantactis.* Notwithstanding the simplified branchial skeleton and the paucity of its muscles, an important and peculiar mechanism has been developed from this decadent inheritance.

From the mechanical relations of their origin and insertion the various branchial muscles concerned with the swallowing mechanism apparently function as follows. Preparatory to striking the pharyngeal fangs into prey contraction of the Obliqui dorsales, assisted by the Levatores interni, exserts these teeth forward (fig. 8). This is facilitated when the pow-

Fig. 8 Lateral view of branchial arches and other elements associated with the hypertrophied upper pharyngeals in *Gigantactis.* × 10. Despite the phylogenetic trend toward simplification of these structures in teleosts, a highly developed mechanism to aid in quieting and swallowing large prey has been evolved from these dorsal branchial elements.


ORIGINS M. RETRACT. ARC. BRANCH. SUP.
PARIETAL
ORIG. MM. LEVATORES ARC. BRANCH. EXT. 2+3
EXOCCIPITAL
PROÖTIC
SPHENOTIC
INSERT. M. LEV. ARC. BRANCH. EXT. 3
EPIBRANCHIAL 4
SPINAL CORD
M. LEV. ARC. BRANCH. INTERN. 3
VERTEBRA 3
R. LATERALIS X
R. VISCERALIS X
MM. INTERARC. DORS. 3+4
R. PHARYNGEALIS X
UPPER PHARYNGEALS 2+3
R. BRANCHIALIS X
M. RETR. ARC. BRANCH. SUP.
N. GLOSSOPHARYNGEALIS
EPIBRANCHIALS 2+3
CERATOBRANCHIALS 1-4
INSERT. M. INTERARCUALIS DORSALIS 2
EPIBRANCHIAL 1

erful Levatores externi raise the epibranchials. If the jaw teeth had already seized the victim these latter would probably have to be raised as far as possible for the fangs to be manoeuvered at all. Following this the teeth could then be stabbed downward and forward by the contraction of the Transversus dorsalis anterior. Quieting the struggles of food animals is thus an important function of this apparatus.

Next if the internal levators and the superior retractors of the branchial arches contract simultaneously the impaled prey is pulled back further into the mouth. This process is aided by the inward depressability of the long teeth in the jaws. The final stuffing of the food into the stomach is accomplished by the action of just the retractor muscles which are long and powerful. Since they originate posterior to the skull on the first vertebrae, their "stoking" action is highly effective. From this final position the upper pharyngeals are disengaged from the prey and recover their original position by the combined contractions of the Obliqui dorsales, the Transversus dorsalis and the Levatores externi branchialium.

As suggested above, this extraordinary development of the pharyngobranchial elements has been made possible by the presence or creation of the available space in the cheek region. Three major structural factors are involved here. First, the neurocranium reaches its narrowest extent at the point where the pharyngobranchials lie against it (fig. 3A). Second, the appropriate region of the face has been greatly enlarged by the simultaneous elongation of the snout and the depression of the quadrate-articular joint (fig. 2). Finally, the absence of a Tectum cranii in the orbito-temporal region and of circumorbital elements of the skull as well as the reduced condition of the pterygoid parts combine to leave the necessary room for this swallowing mechanism. These characteristics are associated in turn with the reduced eyes. From a comparison with the morphology of other deep-sea anglers fairly closely related to *Gigantactis,* such as *Dolopichthys,* and *Chaenophryne* (Regan and Trewavas, '32, pp. 34–35), it is clear that the structural changes peculiar to *Gigantactis* in this respect

are: the reduction in breadth of the frontals and their movement toward the mid-line, the elongation of the preoptic region of the skull, and some lateral displacement of the palatine and pterygoid elements. Note that it was precisely these morphological changes which are required to derive the *Gigantactis* skull from a basic larval teleost pattern (fig. 3).

The roof of the mouth is already restricted to thin marginal elements and narrow parasphenoid (like the larval Trabecula communis) in many ceratioids (Regan and Trewavas, '32, section VII) so that this condition is not particularly brought about by the hypertrophy of the dorsal branchial elements. The same comment applies to the reduction of the circumorbital and pterygoid elements. This does not mean, however, that spaces left by these reduced structures are not exploited by the large upper pharyngeals and their muscles, which are thus free to expand into them.

Perhaps the most unusual detail of the above modifications is the narrowness of the dorsal part of the neurocranium in the frontal region. A somewhat comparable situation has been described only in one other form, *Caulophryne* (Regan and Trewavas, '32, p. 42); in *Linophryne racemifera* the same authors (p. 46) report rather similar vacuities in the face but these are produced by the lateral displacement of the palatines rather than a mesiad constriction of the frontals. Unfortunately the work cited gives no information on whether or not these peculiarities are correlated with a specialization of the superior pharyngeal dentition.

C. Basic skull type

In support of the statement made above that the neurocranium of *Gigantactis* is reduced to basic essentials, it is of considerable interest to note its similarities even to developmental stages of primitive teleost skulls (for details of the latter see de Beer, '37). These similarities are illustrated in figure 3, which compares the larval chondrocranium of *Salmo fario,* 9 days after hatching, with the adolescent skull of the

present specimen. Such resemblance of the "adult" characteristics of a descendant to the larval structure of an "ancestor" (referred to as paedomorphosis by Garstang, '22) is actually the reverse of the recapitulation emphasized by Haeckel and his followers (for discussion, see de Beer, '38).

In the present comparison it is clear that there is considerable similarity in the sensory capsules. Both *Gigantactis* and the larval *Salmo* have relatively enormous otic capsules which form a dominant part of the cranium. However, in the latter fish, it has not yet been roofed over in the stage shown. In both forms the nasal and optic capsules are inconspicuous or absent. They will develop in trout into important and large parts of the adult skull whereas in the deep-sea angler they have not done so. In the 16.5-mm trout larva the Tectum cranii is incomplete in the nasal and orbito-temporal regions as it is in *Gigantactis*. These areas as well as the otic become completely roofed over in later stages of trout development. If the preotic tectum forms at any stage of the angler's development, it has secondarily been reduced to the condition found in earlier developmental stages.

The general architecture of the preotic cranium shows marked similarities in *Gigantactis* and the larval *Salmo fario*. The basal part of the snout in the latter consists of the median Trabecula communis bearing anteriorly the ethmoid plate as a fan-shaped expansion. Laterally this is connected with the posterior parts of the cranium by the Taenia marginalis and the pterygoid process of the quadrate. These relationships are closely paralleled in *Gigantactis*. Here the base of the snout consists of the narrow median sphenoid elements bearing anteriorly the ethmo-vomer block. Laterally this is connected with the posterior neurocranium by the frontal-prefrontal, palatine-pterygoid cartilages.

Striking as the similarities of these 2 crania are, several differences between them are also obvious. In the anterior part of the skull the major distinction is the elongation of this region to form the illicial trough in *Gigantactis*. The basal and lateral elements enumerated above are all atten-

uated by this process (fig. 2). In *Lepidosteus* and some other long-snouted fish similar changed relationships have been shown to arise from positive heterogonic growth rates during the developmental period before ossification begins (Needham, '35).

Two further differences result from the intrusion of the hypertrophied upper pharyngeals of the deep-sea angler. The slender frontals are compressed toward the mid-line, while the pterygoid-palatine elements are displaced laterally. The 3 sets of paired arrows (fig. 3B) suggest the displacements of larval structural elements which would be required to produce the *Gigantactis* condition from the basic *Salmo* plan.

While the comparison of neurocrania made above may be instructive, it should be noted that the visceral skeletal of the trout at a developmental stage, where its chrondrocranium resembles the skull of the deep-sea angler, lags far behind the functional system of jaws and gill arches present in the latter fish (fig. 2). Such relative differences in the development of parts in ontogeny are frequent even in fairly closely related animals. They may result from heterochronous differentiation and must be kept in mind when developmental stages of various forms are being compared (de Beer, '37, p. 447). Only a study of its ontogeny could demonstrate with certainty whether the strikingly elementary features of the *Gigantactis* skull are a primary or a secondary acquisition in its development. There is no doubt that they are phylogenetically a secondary simplification (see Gregory, '33, p. 390 ff).

D. Sense organs

General somatic afferent systems are poorly developed in *Gigantactis*. Dorsal roots of the spinal nerves are smaller in diameter than the corresponding motor roots. But, since several lines of evidence cited above indicate marked limitation of locomotor activity, the relative size of these roots implies an even poorer sensory inflow over spinal pathways. The absence of external lobes in the dorsal cervical region of

the *Gigantactis* spinal cord indicates further that the cutaneous sensitivity of the pectoral fins and surface of the head are less highly developed than they are in *Lophius*. As far as the fins are concerned, this sensory regression is consistent with the decrease in specialization and importance which these pectoral structures have undergone in the evolution of the ceratioids.

An exception to the apparent lack of general cutaneous sensibility occurs in the esca, which is innervated by 2 pairs of large nerves, 1 trigeminal in origin, the other spinal. The evidence is that these are largely sensory in function. In the first place the only effectors known to be present terminally on the illicium are the light organ and some vasomotor elements. Brauer ('08, p. 104) was unable to find nerve endings supplying the luminous gland, but did demonstrate a considerable blood supply to this organ.[5] In the second place the superficial ophthalmic V of teleosts comprises mainly cutaneous sensory fibers plus a few visceral efferent fibers to blood vessels (e.g. *Menidia;* Herrick, 1899). The spinal illicial nerve would likewise be expected to carry a considerable number of somatic sensory neurons and some vasomotor fibers.

The actual demonstration of these visceral efferent pathways is important because they could be used to control the luminescence in the escal light organ (Waterman, '39a). This structure by analogy with comparable organs in certain other fishes (Yasaki, '28; Yasaki and Haneda, '36) and invertebrates (Herfurth, '36) apparently contains symbiotic luminous bacteria which produce the organ's light (Dahlgren, '28). The luminescence of these microöganisms is hightly aerobic (Harvey, '23, pp. 51–52) so that regulation of the O_2 supply would provide a positive control of the otherwise continuous radiation.

[5] In the present dissection the blood supply of the illicium was not observed. However, in a species of *Dolopichthys* whose anatomy will be described in a later paper a large branch of the first efferent branchial artery was found to run onto the fishing filament.

The particular sensory function of the illicial innervation has yet to be determined experimentally. Sensory endings, believed to be gustatory, were found histologically in *Gigantactis vanhoeffeni* supplying the terminal filaments of the esca and knob-like swellings [6] on the surface of the illicial bulb (Brauer, '08, p. 103). No specific sensory cells, such as would form a taste bud were demonstrated. However, experimental work has shown in other teleosts that chemical sensitivity functionally indistinguishable from gustation can be mediated by spinal neurons and without taste buds (Scharrer, Smith, and Palay, '47). Further study of the central origins and details of peripheral distribution of the illicial nerves should be undertaken to resolve some of these interesting problems.

The swelling on the antero-dorsal aspects of the medulla oblongata of *Gigantactis* (fig. 5) may be involved in the hypertrophy of the illicial innervation. Such areas generally continue anteriorly the somatic afferent character of the dorsal horn of the spinal cord. From the facts for *Lophius* (Ariëns Kappers and Droogleever Fortuyn, '09) it is likely that in *Gigantactis* the dorsal parts of the facialis nucleus and the anterior components of the vagus nucleus are implicated.

Judged by its degree of development and size the most important sensory system in *Gigantactis* is the acoustico-lateralis mediated by special somatic sensory neurons coursing through facialis, acousticus, and vagus pathways. The sense organs concerned are those of the lateral line and the inner ear. The former mediate low frequency sound and the perception of thermal and certain proprioceptive stimuli; the latter initiate reflexes concerned with equilibrium, posture, muscle tone and hearing (Pearson, '36). In *Gigantactis* the R. lateralis X is the largest component of this cranial nerve, while facialis and acousticus are also well developed. No detailed study of the neuromast system was made although the peculiar position of some of these sense organs on the rays of the caudal fin was pointed out above.

[6] None of the papillae are present on the esca of *G. longicirra*.

The inner ear (fig. 6) shows no marked peculiarities and is particularly noteworthy only for its relatively enormous size. However, this fact is difficult to evaluate since the functioning of such structures in a physical sense is dependent on absolute rather than relative size. In general no good correlation has been found between the deep-sea habitat and the morphology of the inner ear (Bierbaum, '14). Its structure appears rather to be characteristic of the individual species concerned and the phylogenetic group to which it belongs. On the other hand, the large maculae of the sacculus and lagena and their innervation are of interest in *Gigantactis* since this ventral region of the labyrinth is concerned in most vertebrates with the acoustic, as opposed to the static and equilibratory functions of the inner ear.

In the central nervous system the importance of the acousticolateralis afferents, already implied by highly developed sense organs and their innervation, is further substantiated. The medulla oblongata where such sensory impulses are first relayed is the largest part of this angler-fish's brain (fig. 5).

The remaining special senses in *Giganactis* are poorly developed. As described above for both olfaction and vision, the sense organs, the peripheral nerves, and their central connections all give evidence of considerable regression. The eyes are of particular interest since they would be expected to play a major role in angling. They are, nevertheless, much reduced in size in *Gigantactis*. Even in the shallow water pediculate *Antennarius,* which is apparently close to the center of evolutionary radiation for this order (Gregory and Conrad, '36), the eye is from 2 to 5 times its relative diameter in *Gigantactis* (Longley and Hildebrand, '41, p. 303 ff.) and pediculates in general do not have large eyes for teleosts.

Not only is the light receptor itself much reduced, but accessory and associated elements further imply that vision is a poorly developed sense in this fish. From a kinetic point of view the weak eye muscles and lack of bony orbit contraindicate a vigorous, accurately coordinated mechanism (fig. 1). The optic nerve is thin and the optic tecta, unlike those of

Lophius (Ariëns Kappers and Droogleever Fortuyn, '09), do not form a prominent part of the brain. On the other hand, the optic lobes of *Gigantactis* are not as atrophied as this region of the brain is in blind teleosts (e.g. Charlton, '33).

That such anatomical facts may be interpreted in terms of visual function is supported by several lines of evidence. It has been found by surveying the optic tecta in many teleosts that the degree of development of the visual apparatus is broadly paralleled by that of this relaying center of the brain in lower vertebrates (Lissner, '23). In fishes with well developed eyes and primary dependence on their visual sense, the optic lobes form an outstanding feature of the brain, bulging over the ventral parts of the mesencephalic brain stem and crowding the elements before and behind them (e.g. *Holocentrus,* Meader, '34). But in forms with inherited or acquired (by ablation or disease) deficiencies in their visual organs these receptor shortcomings are reflected in the central nervous system (Charlton, '33, cites a number of examples from the literature).

These relations raise an interesting problem relative to the angling activities in *Gigantactis.* In *Lophius,* a littoral angler, the eyes are quite well developed and strategically situated for covering a wide visual angle around the fishing filament as the fish lies concealed on the bottom. In comparison, *Gigantactis,* with an inconspicuous optic tectum, very slim optic nerve, and a small eye whose visual field appears poorly oriented for surveying the environs of the illicium, seems ill equipped to regulate its angling by visual means. Such considerations emphasize further the desirability of studying the functions of the illicial nerves.

Whatever may be the sensory mechanism which this deep-sea fish uses for detecting and engulfing its prey, the latter presumably must be lured within range by its own visual perception. For if ceratioids use their illicium to attract food organisms, as do their shallow water relatives, it is the luminescence of the esca which makes this possible in the sunlightless depths of the ocean. It is pertinent to recall that many

bathypelagic organisms, both vertebrate and invertebrate, have well developed eyes (Murray and Hjort, '12; Walls, '42), particularly those which live or migrate into the "twilight zone" [7] just below the photic layers of the oceans (Waterman, Nunnemacher, Chace and Clarke, '39). Such normal or hypertrophied eyes are frequently accompanied by highly organized photophores (Chun, 1896; Brauer, '08; Welsh and Chace, '39). Chun (1896) has also pointed out that predators as well as prey would be attracted by light organs. On this account the angler's sensory discrimination must be such that the illicium is not used as an instrument promoting self-destruction.

E. Illicium

In all pediculates the illicium is one of the most interesting structures present. It is no exception in *Gigantactis.* From a morphological point of view the homology of the illicium with dorsal fin rays is a matter of phylogenetic and developmental importance. From a functional point of view the presence of a light organ in the esca and the probable use of the whole structure as a lure for attracting prey are specializations that make it of particular biological significance.

Gigantactis longicirra has a relatively shorter illicium than any other known *Gigantactinidae.* In another species of the genus (*G. macronema,* Regan, '25) this structure is 4 times the length of the body. However, most ceratioids have shorter illicia than do gigantactinids. In *Edriolychnus,* for example, it is a sessile bulb on the surface of the snout. The illicial rod is considerably stouter and less flexible in many anglers (e.g., certain species of *Linophryne*).

The terminal prolongation of the snout in *Gigantactis,* with which the illicial rod articulates, is the basal bone of the illicium. Little or none of it is visible externally in the present specimen, but some or all of this element may be normally

[7] In the region of the oceans where the present specimen was caught this zone extends from about 500 to 800 m; hence *G. longicirra* was living 200 m deeper.

exserted from the body surface as in *Lasiognathus* or *Ceratias* where it is equal in length to the whole body of the fish in certain species (Regan and Trewavas, '32).

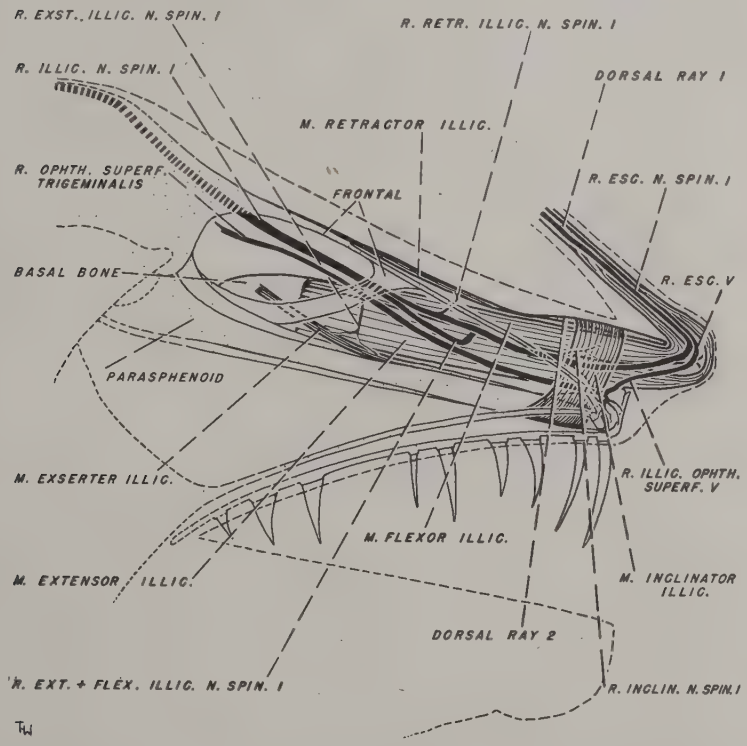


Fig. 9 Lateral view of snout of *Gigantactis* to show details of the innervation of the illicium. × 10. The first spinal nerve, reflecting the post cranial origin of the illicium as the first 2 rays of the dorsal, innervates the 5 pairs of illicial muscles and sends a large branch distally to the esca. In addition the illicium, an adult cranial structure, has acquired a large branch of the R. ophthalmicus superficialis trigeminalis, a condition not previously known in any pediculate.

Another variable in illicial structure which has considerable significance from the point of view of comparative anatomy is its position relative to the rest of the skull. This may be

terminal as in *Gigantactis,* or further caudad to the extreme case of *Lophodolus* where it is not only postoptic in location but even posterior to the sphenotic spines. Since the illicium, as a dorsal fin derivative, must reach its adult position by forward migration onto the skull, it is clear that the further rostrad it moves the more marked will be the modifications associated with its displacement. Thus *Gigantactis* represents an extreme specialization in this respect.

The esca, located terminally, is a final illicial structure which shows marked differences even between species. Its variations in basic plan and details of structure are widely used as taxonomic characters, particularly within a genus. In *Linophryne* and *Dolopichthys,* for example, the numerous species are defined largely by this structure (see the synopses for these genera in Regan and Trewavas, '32, p. 106 and p. 64). The widespread variety in the morphology of such a specialized organ in this teleost suborder suggests that escal details are but weakly selected in the struggle for existence. This would certainly be true if the only functions of the illicium are as a lure for prey and as a sense organ. If, on the other hand, the escal pattern illuminated by its enclosed light organ is used to lure the males (which have no illicium) to females of the appropriate species, such differences could be of survival value. The recognition of sex and species has been given as the function of the wide variations in detail of numbers and arrangement of photophores in the many species of bathypelagic myctophid fishes (Brauer, '08, pp. 161 ff.). In these the pattern established by the light organ or organs would have similar biological significance to recognition devices employed by other animals (Robson and Richards, '36, pp. 148, 292; Noble, '38). Rauther's ('27, p. 165) suggestion that light organs of many twilight-zone fishes are similar in function to protective coloration of surface pelagic organisms (Murray and Hjort, '12, pp. 669 ff.) could not apply to a single localized structure like the escal organ of ceratioids.

Since the general evidence of comparative anatomy as well as the present scant knowledge of the ontogeny of pediculates (*Lophius* is the only form known in any detail: Agassiz and Whitman, 1885; Tåning, '23) indicate that the illicium is the anterior part of the dorsal fin, the homologies of the 3 skeletal elements of this structure are of interest. The illicial rod is quite clearly the first external ray of the fin. The other 2 elements offer some difficulty, however. Typically, the supporting elements of a teleost median fin consist of such an external ray plus an internal structure with which the ray articulates. This is the pterygiophore; basically composed of 3 parts, it may be fused into 1 or 2 pieces in the adult (Eaton, '45). Figure 10A indicates the relation of rays, pterygiophores, and vertebrae in the first 3 segments of *Gigantactis'* soft dorsal. The anterior 2 of these have pterygiophores made up of 2 cartilaginous elements while the third consists of a single piece. Comparison of the overall structure of these normal rays with the illicium is suggestive.

From such a typical fin situation to the illicial ray and basal bone in *Gigantactis* would be a simple step if it were not for the small dorsal element. As Brauer ('08) pointed out the latter lies in the same position as the second dorsal ray of *Lophius* and may reasonably be considered a vestige of that structure. The presence in various pediculates of a series of stages in the degree of development of the second dorsal ray from the condition found in *Histrio* where this second ray is far larger in size and length than the illicium to that found in certain species of *Antennarius* where the illicium itself is considerably the larger, lends support to this belief. Furthermore the constant insertion of certain of the muscles on the second ray and the dorsal illicial element throughout the order as will be described below, also substantiates this notion.

Concluding that the dorsal illicial element is a trace of the second dorsal fin ray complicates the homology of the basal bone with a single pterygiophore. The basal bone may represent the fusion of 2 such ray supports. Sufficiently detailed descriptive embryology of *Lophius* would be the only reason-

ably accessible material for solving this problem ontogenetically.

The homologies of all the illicial muscles are not obvious from the comparative anatomical data. Normally each teleost median fin ray has 3 pairs of muscles: erector, depressor, and inclinator (Harrison, 1895). The musculature of the first soft dorsal rays of *Gigantactis* (fig. 10B) closely follows the typical pattern. However, 5 pairs of muscles are present on the illicium.

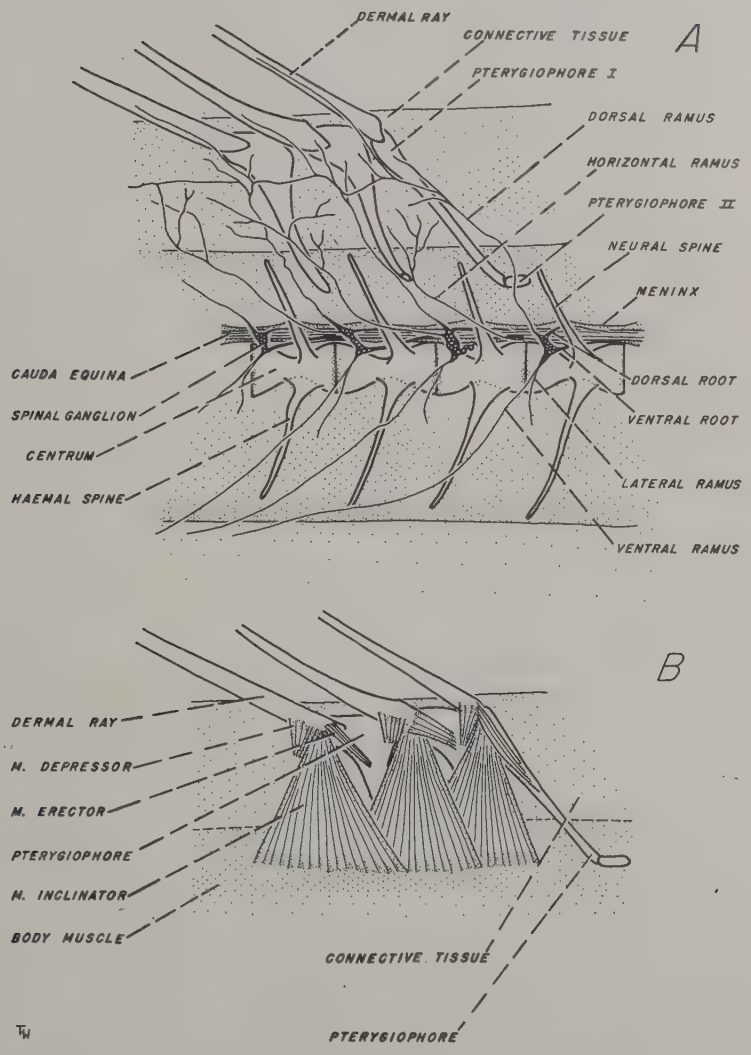
In *Gigantactis vanhoeffeni* Brauer ('08) found only 4 pairs of illicial muscles; no exserter was observed. This apparently was an oversight since all other pediculates where this has been studied have 3 pairs of muscles originating on the neurocranium: inclinator, retractor, exserter (Brauer, '08, except *Gigantactis;* Parr, '30; Regan and Trewavas, '32; preliminary dissections by the author of *Lophius, Antennarius, Histrio, Ogcocephalus*).

Although these muscles which move the illicium relative to the skull are quite stable in their number and action throughout the pediculate group, those which move the parts of the illicium itself are variable. For example, in male ceratioids, which have no illicial ray present as such, the extensor and flexor muscles are lacking (Brauer, '08; Parr, '30). In pediculates where the second dorsal ray emerges externally an additional 2 pairs of muscles are present: depressors and erectors of this ray. Thus 7 pairs of muscles seem to be the primitive number for this whole structure since *Antennarius* possesses this complement and general evidence indicates that this genus lies close to the ancestral type for the Order *Pediculati* (Gregory, '33).

Fig. 10 Skeleton, muscles, and innervation of the first 3 rays of the soft dorsal fin of *Gigantactis*. These are of particular interest for comparison with the modification of parts of the dorsal fin into the illicium.

A. Lateral view of spinal column, fin skeleton, and their relations to the nervous system. × 14.

B. Lateral view showing the 3 pairs of muscles associated with each ray. × 14.


DERMAL RAY
CONNECTIVE TISSUE
A
PTERYGIOPHORE I
DORSAL RAMUS
HORIZONTAL RAMUS
PTERYGIOPHORE II
NEURAL SPINE
MENINX
CAUDA EQUINA
SPINAL GANGLION
CENTRUM
HAEMAL SPINE
DORSAL ROOT
VENTRAL ROOT
LATERAL RAMUS
VENTRAL RAMUS
B
DERMAL RAY
M. DEPRESSOR
M. ERECTOR
PTERYGIOPHORE
M. INCLINATOR
BODY MUSCLE
CONNECTIVE TISSUE
PTERYGIOPHORE
TW

Seven pairs of muscles in the illicium is 1 pair too many to be accounted for by a simple addition of the normal complement of the first 2 rays of the dorsal which the comparative data would indicate is the raw material from which the illicium was developed. Hence an "extra" contractile element is present. This must be either a newly independent part of a normal fin muscle, an element formed *de novo* under the altered conditions, or finally, a cranial (or other) muscle newly acquired by the ilicium and impressed for this service.

Certain of the illicial muscles can be accounted for. The extensors and flexors are quite probably the erectors and depressors of the rays; the inclinator of the second ray (= inclinator of the illicium in *Gigantactis*) is also attached to the derived fin elements as a normal inclinator would be.

This leaves 2 muscles in the primitive pediculate illicium unhomologized (the exserters and the retractors) and 1 basic fin muscle (the inclinator of the first dorsal ray) unaccounted for. The relation of origins and insertions of the retractors are essentially like those of an inclinator (fig. 9) except that their origin occurs far posterior to the adult position of even the second fin ray or its vestige. However, the possibility that anchorage of the muscles to cranial structures may take place before the illicium has reached its terminal position should not be overlooked. The final configuration would then be produced by traction on the developing muscle, resulting from the continued forward migration of the illicium.

In *Gigantactis* with only 5 pairs of muscles present the situation seems simpler. But it is fundamentally the same since the 2 pairs apparently not present are the erectors and depressors of the second dorsal ray. Hence the uncertainties remain concerning the exserters, retractors, and the inclinators of the first ray. Developmental studies of the differentiating illicium, even in *Lophius,* would probably resolve these questions of homology for the whole group.

The migration of the illicium of *Gigantactis* to a terminal position on the snout from its ontogenic and phylogenetic origin as dorsal fin rays on the body provides a natural

experiment on the nature of some of the factors determining morphogenesis. Not only have the skeleton and muscles of the fin rays been influenced by this translocation, but in addition the neurocranium, brain, and certain spinal and cranial nerves have all undergone deformation or displacement in the process. Three pairs of modified dorsal fin muscles now have their origins on the skull, large parts of the first spinal nerve innervate adult cranial structures, and the trigeminal nerve supplies a thick branch to a structure derived from postcranial elements. Thus the developmental factors which effected these complex innovations must involve movement and heterochronous growth rates in many different tissues of the fish's body.

In the ontogeny of this angler-fish the first rays of the dorsal fin apparently established relations with dorsal rami of spinal nerves as these rays normally would. Then as the differentiating illicium moved forward relatively late (embryologically) in the course of development, it dragged this spinal innervation with it over the top of the skull out onto the snout. Such towing effects have frequently been described (Weiss, '41) and are of particular interest in the fins of fishes since these structures have undergone marked adaptive radiation. In general median and pelvic fins are innervated by spinal nerves originating in the metameres in which they develop (Goodrich, '13). It is only in particular cases, such as teleosts with jugular pelvics that migrate forward of the pectorals at an ontogenetically late stage in development, that towing phenomena are marked (Hammarsten, '11).

Perhaps more remarkable, since it has not been described before, is the "capture" by the illicium of an extensive cranial innervation. The natural experiment here may be comparable with the laboratory one of inducing innervation of "foreign" sense organs transplanted to a new position in a developing organism (Weiss, '42). On the other hand this trigeminal illicial nerve may rather represent a response to the hypertrophy of part of its regular peripheral sensory field which has been borne out on the esca during illicial development.

The extreme rostral position of the first dorsal ray in *Gigantactis* places the base of its external portion in a strategic location for either of these transformations to occur. A detailed study of the escal sensory endings and their functions would go a long way toward solving this problem. Coupling this with embryological experiments on illicial ablation and transplantation should clear the matter up entirely.

The presence of the large basal bone on the snout of *Gigantactis* has had widespread effects on the neurocranium and perhaps on its contents. As mentioned above the posterior end of the illicial trough forms a concavity in the supraoccipital bone which marks its posterior boundary. Similarly it was observed that the anterior 3 quarters of the brain are apparently so compacted that they lie caudad and ventrad to their typical teleost position and even to their own associated hypophysis and first 7 cranial nerves (fig. 5).

The anterior parts of the skull, conversely, have been considerably elongated in forming the forward portion of the illicial trough. This process, too, has had its repercussions on various cephalic elements. Certain parts of the visceral skeleton are drawn out into long thin structures as a result. Similarly all nerves in the preoptic region of the skull are attenuated. Even the oblique muscles of the eyes are elongated to a fantastic degree by the resulting forward displacement of the anterior myodome. A striking insight into the resulting configuration of the *Gigantactis* extrinsic ocular muscles can be seen in the larval stages of *Salmo fario*. In the 14-mm larva (de Beer, '27, text figs. 43, 44) the oblique muscles originate from the internasal septum far forward in the skull while the recti arise from the posterior myodome and emerge through the hypophyseal fenestra, which lies just ahead of the otic region (Goodrich, '30, fig. 288). The condition shown by this larval salmonid indicates in an illuminating way how a relatively simple elongation of the snout would transform the basic pattern of these relationships into one similar to that found in *Gigantactis*.

The hypophysis of *Gigantactis* would appear to lie in a region of the neurocranium just anterior to the deformations caused by the excavation of the posterior end of the illicial trough and just behind those caused by the elongation of the muzzle. As described above it is located far forward of its normal position relative to the brain to which it remains attached by a long drawn out stalk (fig. 5).

A number of other teleosts are known which also have the hypophysis borne anteriorly in a similar fashion (Lissner, '22, p. 162). In the benthonic pediculate, *Lophius,* this phenomenon has been studied in some detail (Edinger, '11). In a 2-cm specimen of this latter fish the stalk is short and the gland still lies posterior to the optic chiasma; at a length of 15 cm the relations are those of the adult with the hypophysis anterior to the prosencephalon. This unusual relationship is ascribed by Ariëns Kappers, Huber and Crosby ('36, p. 921) to the "peculiar position of the mouth" in this fish, but such a bare statement is hardly self-explanatory. Furthermore, the trigemino-facialis ganglia of *Lophius* also lie partly anterior to the forebrain (preliminary dissection by the author). Such a posterior position of the forebrain relative to both hypophysis and trigemino-facialis ganglia implies a backward movement of the brain after the period in development when the more normal basic relationships were laid down. De Beer ('26, p. 58) suggests that in *Lophius* this modification is brought about by the withdrawal of the brain from the anterior end of the brain case.

An alternative possibility, however, should be considered: namely, that a deformation of the skull at some period of ontogeny may cause the same condition by an active crowding rather than a passive retraction of the anterior end of the central nervous system. Such a distortion of the skull is indeed present in the formation of the illicial trough. This might bring about the observed telescoping of the rostral parts of the brain through the backward and downward movement of the median dorsal skull elements in the supra-occipital region and the area just anterior to it. The critical causal

factors here would be the relative growth of brain and skull modified by the morphogenetic effects of the illicium as it migrates forward to its rostral position.

Now it is known that certain of the organized features of tissues will develop when they are grown apart from their normal living environment (Fischer, '46, pp. 33 ff., 233 ff.). However, there are distinct limitations to this type of "cultured" growth. In particular bone and cartilage organize their basic structural features in the absence of the normal mechanical stresses and relations of parts, but marked changes can be brought about in these basic patterns through the action of such factors (Murray, '36). In fact the differentiation of the skeleton into its adult form is normally conditioned in this way. Hence the mere mechanical effects of a large growing basal bone arriving on the head by rostrad migration could exert the effects observed. Results of extirpating the illicial anlage at various stages would be highly interesting in this respect if experimental material were obtained.

Similarly it is clear that the brain and the brain case have mutually interacting morphogenetic effects (de Beer, '37, pp. 476 ff.). In general the evidence indicates that the teleost cranial cavity restricts the nervous elements in their early stages of development (Ariëns Kappers, '32). If the distortion of the *Gigantactis* skull due to the formation of the illicial trough occurred at this phase in ontogeny, one might expect the observed relationships to be formed. The time factors in the various processes are critical, however, since in the adult teleost the brain may be considerably smaller than its containing cavity. This is so, for example, in *Scorpaena scrofa* (Allis, '09, p. 61). Here the forebrain has apparently "contracted" leaving the trigemino-facialis ganglia ahead of the anterior end of the brain as in *Gigantactis*, but in *Scorpaena* the hypophysis retains its normal relations to the infundibulum.

It has been shown experimentally (Nicholas, '30) that rapidly growing cranial contents, conversely, can cause an expansion of the skeletal elements enclosing them. From the

foregoing it is clear that the relative growth rates and morphogenetic powers of the various elements involved may change markedly at different stages in development. Experimental knowledge of these forces and relations are essential to further analysis of the problem.

Most of the foregoing discussion has emphasized those characteristics of *Gigantactis longicirra's* anatomy which have been influenced by the fish's deviation from the basic spiny-finned type. It may be well to point out in closing that one of the central regions of the angler's skull, namely the inner ear (fig. 6) and the surrounding otic capsule (fig. 3A) have been highly conservative. They form a major portion of the large head, yet have been little modified by the morphogenetic factors which have influenced neighboring structures. The same is true of the posterior part of the brain stem which is contained within. In a figurative, as well as a literal sense, these conservative features have been an anchor on which more labile and affected elements have depended.

Obviously a number of unanswered questions of considerable interest have been raised during this analysis of *Gigantactis'* anatomy. Answers to the most promising of these will probably be forthcoming only from a concerted attack on the problem from the points of view of physiology and experimental embryology as well as that of comparative anatomy.

V. SUMMARY

1. *Gigantactis longicirra* Waterman is a highly specialized pediculate teleost of the Suborder *Ceratioidea* Regan.

2. The anatomical material described is limited to the type specimen, which was taken at 1000 meters depth in the Western North Atlantic.

3. For a deep-sea angler-fish, *Gigantactis* has a slim and elongate body with a moderate head bearing the illicium terminally.

4. Little bone is present in the skeleton in which many of the elements are weakly developed and attenuate.

5. The cranium is basically simple in structure with its special features conditioned by 2 peculiarities: (a) presence of the first 2 dorsal fin rays on the snout, (b) hypertrophy of the dorsal parts of the second and third branchial arches.

6. The pectoral girdle is mechanically weak and unbraced while the fin itself is a reduced pediculate structure located high on the sides of the body.

7. Five radialia, one more than is known in any other pediculate, are present in the pectorals.

8. The illicium consists of 3 skeletal parts (basal bone, illicial ray and a small dorsal element) and is moved by 5 pairs of muscles.

9. Muscles activating the enormous upper pharyngeal teeth are well developed, despite their reduced number compared with most teleosts; particularly large are the Retractores arcuum branchialium superiores.

10. The digestive tract is short and unconvoluted; no pyloric caeca are present.

11. Highly tortuous blood vessels course over the surface of the sac-like stomach.

12. The swim bladder is absent.

13. The heart and 4 branchial arches present a typical teleost pattern.

14. The renal portal system appears highly inclusive; even the brachial veins enter the kidneys before reaching the very elongate ducts of Cuvier.

15. The notably anterior kidneys have little, if any, arterial blood supply; a large urinary bladder is present.

16. All parts of the small brain anterior to the medulla oblongata are relatively reduced in size and compacted together so that the anterior end of the forebrain lies behind the hypophysis, the trigemino-facialis ganglia, and the crista of the anterior semicircular canal.

17. The adenohypophysis is connected by a much elongated stalk to its usual origin, the hypothalamus.

18. Optic lobes and cerebellum are weakly developed.

19. The only large cranial nerves originate from the medulla oblongata: V, VII, VIII, X; the rest: I, II, III, IV, VI, and IX are quite attenuate.

20. A large branch of the superior ophthalamic of the trigeminal innervates the terminal part of the illicium; this cranial innervation of a dorsal fin structure had not been observed in pediculates before.

21. R. lateralis vagus is the largest branch of the tenth cranial nerve.

22. The eye is much reduced in size, being only 1/50 of the standard length of the fish.

23. The labyrinth of the inner ear is relatively enormous; no Canalis sacculi-utriculi or Macula neglecta is present.

24. The spinal cord tapers rapidly to a Filum terminale; from about the fourth vertebra caudad the central nervous system consists of a Cauda equina.

25. The first spinal nerves are double and innervate both the illicium and part of the pectoral girdle and fin.

26. Spinal illicial nerve provides all the innervation to the 5 pairs of muscles in the illicium as well as a large branch which accompanies the ramulus of the trigeminal superior ophthalmic to the esca at the tip of the illicium.

27. Remaining spinal nerves have elongate roots, the motor root always being the larger, and divide into 4 rami in typical teleost fashion.

28. From the evidence of body and pectoral fin musculature, the attenuate pectoral girdle, the position of the pectoral, absence of pelvics, and the inconspicuous nature of the cerebellum, it is concluded that *Gigantactis* is a weak swimmer.

29. Adaptation as a floating bathypelagic trap has modified many of this angler's structural characteristics: posterior elongation and enlargement of the branchial cavity have displaced the pectorals; specialization of the dorsal branchial elements into a powerful mechanism for swallowing prey has had widespread effects on a number of structures in the preotic region.

30. In its basic structure, lack of roofing elements anterior to the otic region, the dominance of the inner ear and its capsule, and absence of optic and nasal skeletal parts, the neurocranium of *Gigantactis* is shown to have a striking similarity to the developing chondrocranium of *Salmo fario*.

31. General somatic afferent systems, except perhaps in the cranial and spinal innervation of the illicium, are poorly developed in *Gigantactis;* evidence from sense organs, nerves, and the gross structure of the brain and spinal cord indicates that the major sensory inflow of this fish is the acousticolateralis.

32. The function of the generous innervation of the esca is of particular interest in view of the problem of controlling its luminescence and the implied use of the illicium by the fish as a lure for its prey.

33. Special senses of olfaction and vision are poorly developed, facts which are noteworthy in connection with the problem of food getting in general and with angling for prey with a light organ in particular.

34. The presence of the illicium on the skull also has considerable morphogenetic interest because of its widespread effects on skeleton, muscles, nerves, and central nervous system.

35. Analysis of the homologies involved shows that, not only have the old elements been translocated and put to new uses, but also new ones have, like the trigeminal illicial nerve, been acquired and integrated with the old basic pattern; the original derivation of the illicium apparently includes the second dorsal fin ray as well as the first plus their associated nerves and muscles.

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Contribution No. 433

Reprinted from THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA, Vol. 20, No. 3, 305–309, May, 1948
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Reflection of Sound from Coastal Sea Bottoms*

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(Received December 18, 1947)

An experimental method has been developed for measuring the reflection coefficient of the ocean bottom for supersonic sound at grazing incidence. In this method the geometry is controlled so that the resultant of the direct and reflected rays passes through consecutive maxima and minima at the hydrophone. The amplitude reflection coefficient is given by the expression $(M-m)/(M+m)$, where M is the amplitude of a maximum and m is the amplitude of the following minimum. Using this method, with a grazing angle of nine degrees, the following values were obtained for the reflection coefficients at 17 stations near Woods Hole: *mud*—0 to 0.20, *mud-sand*—0.20 to 0.40, *sand-mud*—0.40 to 0.60, *sand*—0.40 to 0.85, *stony*—0.50 to 0.85. It is observed that the reflection coefficient depends not only on the median size of the particles making up the bottom, but also on the sorting of the particles and on the bottom topography.

I. INTRODUCTION

IN the past few years considerable interest has been aroused in the study of the ocean as a medium for transmitting sound. In addition to the medium itself, its boundaries, namely the ocean bottom and surface, play an important role in the propagation of sound. Both the surface and the bottom act as acoustical reflectors; a sound ray striking the bottom or the surface will be partly reflected. It was the purpose of this study to investigate the properties of ocean bottoms as acoustical reflectors. Surface reflectivity will be discussed in a forthcoming paper. The sound frequency, 24 kilocycles, was selected as being the most useful for current application of the results. All of the reflection data were obtained *in situ* by making measurements from a specially equipped ship operating in coastal waters in the vicinity of Woods Hole, Massachusetts.

It is to be expected that the reflection coefficient would vary widely depending on the nature of the bottom. Mud, for example, would be expected to absorb a large fraction of the incident sound and reflect only slightly; sand might be expected to absorb only slightly and reflect very well. The bottom samples taken at each station provided a means not only of checking such general expectations, but also of exhibiting any correlation that might exist between the size distribution of the particles on the bottom and the reflectivity of the bottom as a whole.

The following sections give, in turn, the elementary theory underlying the experiment: the experimental and analytical procedures employed; measured bottom reflection coefficients at various stations; and, finally, a discussion of the effect of geometric irregularities.

II. ELEMENTARY THEORY OF REFLECTION MEASUREMENTS

A projector and receiver are placed about 60 feet apart, at a height of a few feet above the ocean bottom. If the sea surface is assumed to be infinitely far away, sound from the projector reaches the receiver in two distinct ways; it travels directly through the water, and it strikes the bottom and is reflected to the receiver. If the bottom is perfectly plane and the projector and receiver considered as points, only one ray will be reflected to the receiver; but if the bottom is irregular, sound reaching the bottom at other points may also be reflected to the receiver. In this section we shall assume that the bottom is perfectly plane, so that the reflected ray is unique. It will be shown in Section V that the reflection coefficients calculated with these simplified assumptions also have a valuable meaning in the more general case.

A formula for the bottom reflection coefficient may be derived in the following manner. Let d = amplitude of the direct ray at the receiver, r = amplitude of the reflected ray at the receiver,

* Work carried out under Contract NObs-2083 for Bureau of Ships, Navy Department.
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† Contribution No. 433.

θ = phase angle between direct and reflected rays at receiver, ρ = amplitude reflection coefficient of the bottom (ratio of amplitude after reflection to amplitude before reflection), R = resultant amplitude of sound reaching receiver, M = maximum value of R, and m = minimum value of R.

We shall examine first the case where the projector and hydrophone are both non-directional in the vertical plane. For an arbitrary value of the phase angle θ, R is related to d and r by the usual formula

$$R=(d^2+r^2+2dr\cos\theta)^{\frac{1}{2}}. \tag{1}$$

The weakening of the direct and reflected rays resulting from geometric divergence can be taken as the same, because of the approximate equality between the lengths of the two paths. Thus the amplitude r differs from the amplitude d only because of loss of sound to the bottom; and the two amplitudes are related by

$$r=\rho d, \tag{2}$$

because of the definition of the bottom reflection coefficient. Thus Eq. (1) becomes

$$R=d(\rho^2+2\rho\cos\theta+1)^{\frac{1}{2}}. \tag{3}$$

In this experiment the phase angle θ between the direct and reflected rays was constantly varied by changing the height of the projector. Equation (3) shows that under these conditions the resultant sound R will pass through extremes of maxima and minima amplitude. Maximum amplitude will be obtained when the reflected and direct rays are in phase ($\theta=m\pi$, m even). Minimum amplitude will occur when the direct and reflected rays are exactly out of phase ($\theta=m\pi$, m odd).

The maximum resultant amplitude M, is then given by

$$M=d(1+\rho),$$

and the minimum resultant amplitude, m, is

$$m=d(1-\rho).$$

From these we get

$$M/m=(1+\rho)/(1-\rho),$$

or, solving for the reflection coefficient ρ,

$$\rho=(M-m)/(M+m). \tag{4}$$

In order to eliminate the possibility of surface reflected sound influencing the results, transducers were selected which were somewhat directive in the vertical plane. This directivity decreased the amplitude of the bottom reflected ray, but much less than the surface ray owing to the very small grazing angle (9°). Equation (4) can be easily corrected for the vertical directivity of the transducers. Let K_1 be the ratio between the amplitude of the sound projected along the horizontal and the amplitude of the sound projected at nine degrees; and let K_2 be the analogous ratio for the hydrophone. Then Eq. (2) must be replaced by

$$r=K_1K_2\rho d, \tag{5}$$

and Eq. (4) becomes

$$\rho=[1/K_1K_2][(M-m)/(M+m)]. \tag{6}$$

As will be shown in Section III, neglect of the correction factor $1/K_1K_2$ will not significantly increase the error of the result.

III. EXPERIMENTAL AND ANALYTICAL PROCEDURES

Two large ring stands with bases approximately eight feet in diameter carried the projector and hydrophone. These ring stands were sufficiently heavy so that while on the bottom it was impossible for them to move in any direction. Since the two stands were lowered from an anchored vessel at points in the bow and stern 60 feet apart, the nominal projector-hydrophone distance is 60 feet; but some unavoidable ship motion between the two lowerings could put this 60-foot estimate in error by as much as 20 feet.

The projector used was of the magnetostriction type, and was sufficiently non-directional in the horizontal plane so that sound sent out in all directions is constant to within 3 db. This characteristic, along with a similar approximate non-directionality of the receiving hydrophone, insured that the received signal would be well above background noise no matter what the orientations of the sending and receiving racks. The projector was somewhat directional in the vertical plane, having an effective vertical width of about one inch. With the distances used in this experiment, a rough calculation shows that the value of K_1, in Eq. (6) is between 0.95 and 0.99.

The vertical steel rack holding the projector was driven by a pinion gear and electric motor. By means of this setup, the projector was driven between the heights of 56 inches and 80 inches above the bottom, covering this distance in about 80 seconds. The motor used for increasing or decreasing the height of the projector was controlled from the experimental vessel. In a typical run, lasting about 2.7 minutes, the projector was started in its lowest position, driven to its highest position, and then driven back to its lowest position again. With this geometry, the interference pattern for a complete run would be expected to include several cycles.

The receiving hydrophone was rigidly held 56 inches from the bottom. A Bell Laboratories unit D-170249 magnetostriction hydrophone was used because of its naturally broad vertical beam pattern. The receiver face of the hydrophone had a width of one inch. Thus K_2 in Eq. (6), as well as K_1, is limited to the range 0.95 to 0.99, so that the correction factor $1/K_1K_2$ is in no case greater than 1.10. Since the minimum amplitudes on the film could not generally be read with an accuracy much better than ten percent, the simpler Eq. (4) was used for the computation of bottom reflection coefficients.

The projector was driven by an inverse feedback 16-watt amplifier possessing excellent output voltage stability. The sound energy was initiated by a Hewlett-Packard Model 2C oscillator, which in all cases was tuned to 24 kc. The connection between the oscillator and amplifier was made intermittently by an automatic keyer which gave eight pulses of 24 kc sound each second, each pulse approximately 30 milliseconds in duration.

The output of the hydrophone was fed into a conventional resistance coupled amplifier whose output in turn was fed into a cathode ray oscillograph having a short persistence screen. A continuously moving film camera was set up to photograph the oscillograph deflections, using a slow film speed of about six inches per minute. By means of this slow film speed, the record of each received ping was compressed to a thin vertical line; and a complete run, comprising over 1000 pings, was portrayed on 18 inches of film. Film records of typical runs are shown in the next section.

Samples of the bottom sediments were taken at various points on the bottom at each station, and later carefully analyzed in the laboratory in order to determine the distribution of particle size. Each such set of bottom samples was then given a designation of the type used in the U. S.

TABLE I. Summary of reflection coefficients and bottom sample data for all stations. (Reflection coefficients measured at 24 kc.)

Station number	General bottom type	Particle size distribution (mm)				Number of reflection coefficients	Individual reflection coefficients	Average reflection coefficients
		Upper quartile	Median	Lower quartile	Sorting coefficients			
1	Mud	0.026	0.011	0.0024	3.3	5	0.14, 0.20, 0.12, 0.17, 0.20	0.17
2		0.028	0.013	0.0044	2.5	2	0.15, 0.16	0.16
3	Mud-Sand	0.038	0.014	0.0033	2.3	3	0.21, 0.20, 0.23	0.21
4		0.040	0.015	0.004	3.1	3	0.41, 0.29, 0.30	0.33
5		0.082	0.026	0.0045	4.3	4	0.44, 0.31, 0.33, 0.37	0.37
6	Sand-Mud	0.38	0.25	0.12	1.8	5	0.47, 0.49, 0.41, 0.47, 0.40	0.45
7		0.45	0.28	0.11	2.0	7	0.41, 0.46, 0.46, 0.55, 0.43, 0.60, 0.61	0.50
8	Sand	0.63	0.26	0.23	1.7	5	0.52, 0.48, 0.47, 0.53, 0.55	0.51
9		0.49	0.27	0.23	1.5	5	0.79, 0.80, 0.75, 0.72, 0.69	0.75
10		0.41	0.30	0.20	1.5	6	0.72, 0.68, 0.75, 0.68, 0.71, 0.64	0.70
11		0.69	0.46	0.25	1.7	4	0.86, 0.82, 0.85, 0.86	0.85
12		0.72	0.58	0.39	1.4	4	0.58, 0.69, 0.58, 0.58	0.61
13		0.71	0.58	0.45	1.3	5	0.49, 0.47, 0.61, 0.48, 0.65	0.54
14		0.82	0.59	0.33	1.6	3	0.38, 0.42, 0.43	0.41
15	Stony	7.80	1.00	0.58	3.7	3	0.47, 0.67, 0.54	0.56
16		1.55	1.04	0.69	1.5	5	0.49, 0.47, 0.48, 0.56, 0.57	0.51
17		24.0	1.40	0.29	9.1	2	0.85, 0.80	0.82

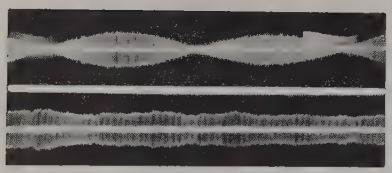

FIG. 1. Portions of typical records showing interference patterns over two different types of bottoms: *a*, sand; *b*, mud.

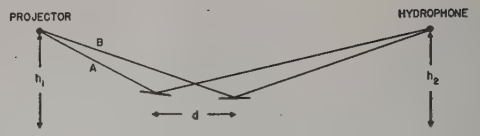

FIG. 2. Simplified irregular bottom.

Navy Hydrographic Office Bottom Sediment Charts, according to the following criteria:

Mud—90 percent or more of the set of samples (by weight) made up of particles with diameter less than 0.062 mm,

Mud-sand—51 to 90 percent made up of particles smaller than 0.062 mm in diameter,

Sand-mud—10 to 50 percent made up of particles smaller than 0.062 mm in diameter,

Sand—less than 10 percent made up of particles smaller than 0.062 mm, at least 90 percent made up of particles smaller than 2.0 mm,

Stony—clastic material consisting mainly of pebbles and cobbles, and

Rock—bottom mainly rock outcrop or covered with boulders.

The next section will describe the correlation between the measured reflection coefficient and the observed bottom characteristics.

IV. CALCULATED REFLECTION COEFFICIENTS

In order to be certain that the reflection coefficient measurements were representative of the station area rather than for some highly localized area, only those stations were occupied which a sediment analysis showed to be uniform in bottom throughout the working area. These comprised two stations over *mud*, three over *mud-sand*, two over *sand-mud*, seven over *sand*, and three over *stony*. Table I gives the bottom information and the calculated reflection coefficients for each of the stations, while Fig. 1 shows portions of typical interference patterns received over various bottom types.

In general, the reflection coefficients shown in Table I do not contradict the assumptions which have been made concerning bottom reflectivity. *Mud* is the poorest reflector, *mud-sand* nearly as poor, *sand-mud* appreciably better, and *sand* the best reflector of all; *stony* bottoms are better reflectors than *mud* but worse, in general, than *sand*. Numerically, the reflection coefficient for *mud* may be expected to lie between 0 and 20 percent;* for *mud-sand*, between 20 and 40 percent; for *sand-mud*, between 40 and 60 percent; for *sand*, between 40 and 85 percent; for *stony*, about 50 percent for most, but much higher for a level smooth *rock* bottom. The major part of the spread of the reflection coefficients for any one station is accountable for by the nature of the bottom topography. Since bottoms are not perfectly plane, the reflection coefficient measured for the projector at one height would not be expected to exactly reproduce the coefficient measured at another projector height. This effect of bottom irregularities will be considered in detail in Section V.

The reflectivity of a boundary between two media depends on the densities of the two media, the elasticities of the two media, and the grazing angle of the incident sound. Unfortunately, conventional bottom sampling techniques do not include provisions for measuring either the density or the elasticity of the material composing the bottom. However, there is one quantity determinable directly from the particle size distribution which might be related to the reflectivity. This quantity is the sorting coefficient P, defined as $P=(q_3/q_1)^{\frac{1}{2}}$ where q_3 is the upper quartile and q_1 is the lower quartile. One might expect that for bottoms consisting of small particles, the greater the sorting coefficient, the greater would be the reflectivity; the smaller particles would fill in the interstices between the larger particles, and so increase the acoustic "hardness" of the bottom. This expectation is fulfilled for the *mud-sand* and *sand-mud* bottoms. The sorting coefficients for each of these two

* In a run at one station, which unfortunately could not be included in Table I because the bottom sample was lost, the reflection coefficient was significantly zero.

bottom types (see the sixth column of Table I) increases as the reflection coefficient increases. No such correlation is evident for the *sand* bottoms, while for *stony* bottoms the sorting coefficient would be expected to have little acoustic significance.

V. REFLECTION FROM IRREGULAR BOTTOMS

Perfectly plane coastal sea bottoms would be expected to be just as rare as perfectly plane areas on land. Though approximately level areas of the bottom are common and, indeed, are sought out in these experiments, small-scale irregularities of dimensions as small as a few inches may cause the reflection of 24 kc sound to be quite different from the mirror-like reflection assumed in Section II. There is ample evidence that irregularities this large and larger occur in practice. Some sea bottoms, such as *stony* and *rock*, obviously are not smooth. Other bottoms, like *sand* and *sand-mud*, may or may not be smooth, depending on ocean currents.

An exact treatment of the reflection from an irregular surface may be given only if the geometry of the surface is completely specified. Ornstein[1] and, more recently, Eckart[2] have given mathematical treatments of such reflection using various assumptions concerning the statistical distribution of the surface irregularities. However, the distribution of these irregularities cannot be measured by any obvious method.

A simplified picture of how bottom roughnesses may influence the interference pattern may help in understanding some of the results given in Section IV. Suppose the bottom topography is such that the hydrophone receives sound reflected from two small plane areas, separated by a distance d, and does not receive sound from any other portion of the bottom. This situation is pictured in Fig. 2. If a is the amplitude of ray A at the hydrophone and b of ray B, the resultant amplitude for the reflected ray will be

$$r=(a^2+b^2+2ab\cos\theta)^{\frac{1}{2}}, \qquad (7)$$

where

$$\theta=(2\pi/\lambda)(\textit{Path length } A-\textit{Path length } B).$$

For the case of a smooth plane bottom, the amplitude of the reflection ray was given by the simpler expression (2).

If the dimensions of the two reflecting planes are small, of the order of a few wave-lengths of 24 kc sound, the two mirrors will continue to deliver sound to the receiver even when vertical motion of the projector changes the geometry. However, as the projector height changes, the amplitude at the hydrophone will vary in amplitude as h_1 varies because the phase difference between the reflected components depends on h_1.

In actuality, the bottom reflections would rarely come from two small plane areas as in the preceding example, but would come from many such plane areas. However, though the mathematics for the general case would be much more complicated, qualitatively the results would be the same. The reflected ray would vary in amplitude according to the topography of the bottom and the relative positions of projector and hydrophone, and the resulting interference pattern of the total received sound would show the result of this fluctuation.

The essential truth of this simple picture is confirmed by the film records, showing the amplitude of the received sound as the projector is driven from low position to high position and back to low position. In all of these records, the interference pattern is very nearly symmetrical about the amplitude corresponding to the highest projector position. That is, though successive minima do not reproduce, the minima corresponding to the projector at a given height do reproduce. For such records, it must be presumed that the observed pattern is caused by the perturbation of the theoretical pattern by irregularities of the bottom topography.

The author was assisted in this work by Mr. Robert Cottell who shared a large part of the field work and Mr. Arthur Yaspan who assisted with the analysis of the records.

[1] L. Ornstein and R. Van der Berg, Physica, **4**, 1181 (1937).
[2] C. Eckart, to be published.

Contribution No. 434

Reprinted from Biological Bulletin, Vol. 94, No. 3, 236–243, June, 1948
Printed in U. S. A.

SEASONAL AND ANNUAL VARIATIONS IN THE ATTACHMENT AND SURVIVAL OF BARNACLE CYPRIDS [1]

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Two factors governing the development of a barnacle population have been investigated: namely, the number of barnacle cyprids attaching daily and the relationship of the daily cyprid accumulation to the number of adult barnacles attaching per month in Biscayne Bay, Miami Beach, Florida. On surfaces exposed for one month at this location, adult barnacles were invariably the dominant organism. No competition by other forms developed in this time interval to limit significantly the attachment of barnacles or their growth. This study was therefore concerned with numbers of cyprids settling daily, survival of cyprids, seasonal growth rates and space limitations, as factors affecting the size of the month-old barnacle population.

The survival of barnacles following attachment has been studied principally by Moore (1934), Hatton (1938) and Moore and Kitching (1939) with respect to the attachment of *Balanus balanoides* and *Chthamalus stellatus* to cleaned rock surfaces in the intertidal zone. These investigations were interested mainly in the effect of tidal level, exposure to surf and to sun, and interspecific competition on the growth and mortality of intertidal barnacles. Their findings are not directly applicable to barnacles attached to continuously submerged surfaces since they emphasize the effect of tidal exposure. The investigations of van Breemen (1933) on the survival of barnacles attached to continuously immersed surfaces considered the ultimate age of specific species.

Methods

To ascertain the numbers of barnacle cyprids attaching daily, a collecting surface of smooth, black glass was hung in the waters of Biscayne Bay at the Beach Boat Slips, Miami Beach, Florida, just below the low-tide mark. The cyprids which attached to one side of the glass (500 sq. cm.) during each 24-hour period were counted daily between 8:00 A.M. and 8:15 A.M. The surface was wiped clean after each counting. Temperature and density of the surface water were also determined at the same time. From these data salinity was calculated. The investigation was carried out over a period of 38 months, except for short interruptions in the summers of 1943, 1944 and 1945.

[1] Contribution No. 434 from the Woods Hole Oceanographic Institution. The observations were made during an investigation by the Woods Hole Oceanographic Institution under contract with the Bureau of Ships, Navy Department, which has given permission for their publication. The author is indebted to Dr. A. C. Redfield, Dr. B. H. Ketchum and Dr. W. T. Edmondson for helpful advice and criticism. The assistance of Mr. Alexander C. Frue in the collection of the data is gratefully acknowledged.

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During the same period, monthly fouling attachments in Biscayne Bay were also reported. These fouling collections were made on clear glass panels, backed with a dark red paint, of the same area as the cyprid collecting surface. The dark red backing provided a substratum color which was comparable to the black glass (Visscher and Luce, 1928). A total of 74 monthly collections were made, panels being immersed every 15 days for 30 days of exposure. From the monthly attachment of assorted fouling forms the barnacle count was extracted for comparison with the sum of the daily cyprid attachment for the same month. *Balanus improvisus* was the dominant adult barnacle on the monthly collectors and presumably was responsible for most of the cyprids (Weiss, 1948).

Results

The daily records of cyprid attachment, water temperature and salinity are presented in Figures 1, 2 and 3, respectively. Three-day moving averages were employed in plotting these data, for the purpose of minimizing random fluctua-

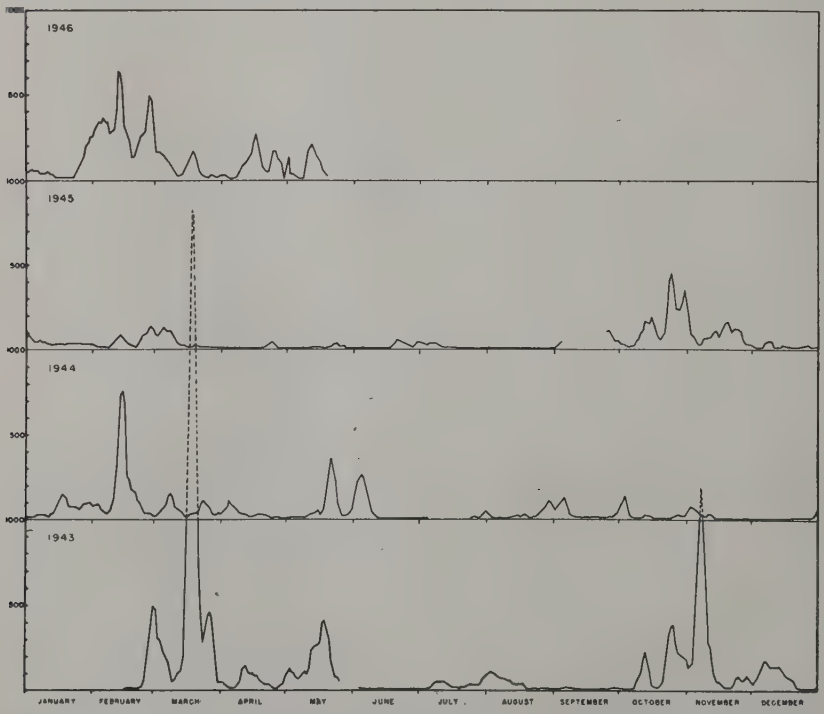

Figure 1. The daily accumulation of barnacle cyprids on black glass (500 sq. cm.) at the Beach Boat Slips, Miami Beach, Florida, February 1943–May 1946, plotted as a three-day moving average.

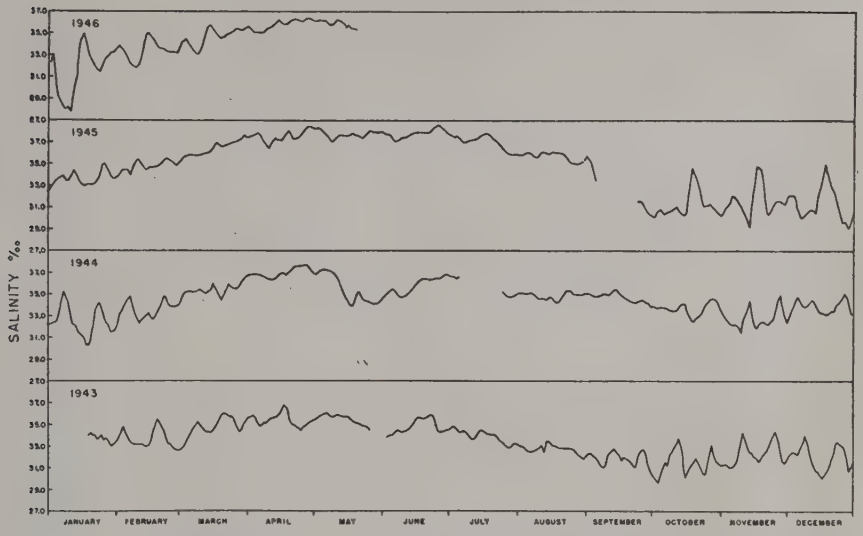

FIGURE 2. The daily salinity record of Biscayne Bay made at the Beach Boat Slips, Miami Beach, Florida, plotted as a three-day moving average.

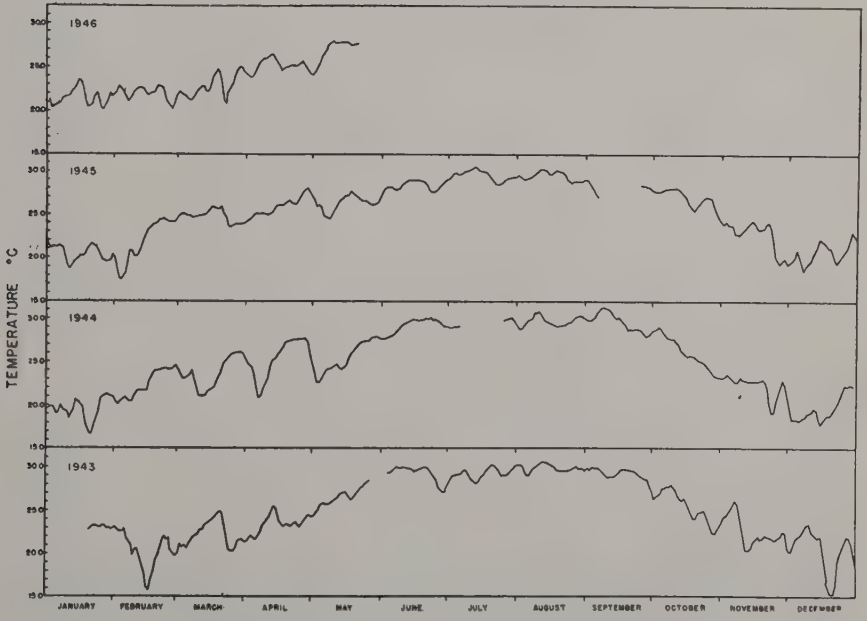

FIGURE 3. The daily temperature record of Biscayne Bay made at the Beach Boat Slips, Miami Beach, Florida, plotted as a three-day moving average.

tions. Both the temperature and salinity of Biscayne Bay showed seasonal variation. The temperature fluctuated each year between approximately 16° C. and 30° C. The salinity showed an annual range from approximately 28.00 $^{o}/_{oo}$ to 37.00 $^{o}/_{oo}$, the peak coinciding with the end of the dry season. This period occurred each year between April and June. With the onset of the summer rains, the bay salinity declined, reaching its minimum in the period from October to January. During this period, and to a lesser degree in the month preceding and following, the salinities showed marked short-period fluctuations, which were indicative of the stage of tide at which the water sample was taken. A sample taken at high tide was always more saline than one sampled at low tide. This fluctuation of salinity was most pronounced during the rainy season, when the surrounding land areas were well soaked and the fresh water run-off from the land diluted the bay water. Slight tidal variations in salinity were evident even in the period of maximum salinity, but the range was not as great. Temperature fluctuations paralleling the tidal cycle were also evident due to the more rapid warming and cooling of the comparatively isolated bay water.

Barnacle cyprids settled on every day but three during the 38 months of observation. The numbers attaching daily varied from as low as 1 or 2 to a maximum of over 2800 per 500 sq. cm. In general, the settling of cyprids was characterized by peaks in attachment at relatively frequent intervals. Nevertheless, there was no apparent relationship between the sizes of successive peaks and the interval between the peaks, which ranged in most cases from 7 days to a month.

Several peaks of cyprid attachment occurred in the early spring and late fall of each year, but these peaks showed considerable variation from year to year in both magnitude and exact time of occurrence. The period from June to September was characterized by low daily cyprid attachments and a few small peaks, if any. However, in 1945 this period of reduced daily attachment extended from the middle of March to September. The spring peaks of attachment were generally greater than those of the fall; but in 1945 this pattern was reversed, the fall peaks being greater. The spring peaks in 1946, although large, were not as great as in 1943 and tended to extend over a longer period.

For the purpose of ascertaining the mechanism controlling the periodic rises in cyprid attachment, these fluctuations were analyzed with respect to changes in the temperature and salinity of the bay water. Since the barnacle cyprid follows after a series of six nauplii stages, fluctuations of its attachment were also examined with respect to changes in the marine environment taking place at the time of release of the nauplii into the plankton. A search of the literature failed to reveal the duration of the free-swimming period for *Balanus improvisus*. However, of the species that were studied (Table I), the free-swimming periods ranged from 7 days to 3½ weeks.[3]

Assuming intervals of one, two or three weeks between spawning and settling, no satisfactory correlations were found between changes in temperature and salinity and the periodic peaks in cyprid settling. The only relationship evident was between the seasonal increases in numbers settling and the temperature. The rises

[3] The period of time that the cyprid spends in the plankton prior to settling was noted quantitatively by Willemoes-Suhm (1876), who studied the development of *Lepas fascicularis*. In addition to observing six nauplii stages, he noted that the "cyprid evidently attaches itself on the very first occasion."

TABLE I

Time for development through nauplii stages to cyprid

Barnacle species	Number of nauplii stages	Time for development to cyprid
Balanus crenatus Bruguiere [1]	6	7–10 days
Balanus crenatus Bruguiere [2]	8	13–14 days
Balanus eburneus [3]	6	7–10 days
Balanus perforatus Bruguiere [4]	6	21 days
Chthamalus stellatus [5]	6	18–20 days
Verruca stroemia [5]	6	23–27 days
Balanus balanoides [5]	6	3–3½ weeks

[1] Bohart (1929). [3] Grave (1933). [5] Bassindale (1936).
[2] Herz (1933). [4] Lochhead (1936).

in cyprid numbers in the spring and autumn occurred between the periods of minimum and maximum temperatures. This relationship suggested that *Balanus improvisus* breeds in a temperature range of approximately 18° C. to 27° C. The temperature above which breeding diminished greatly or ceased was more clearly defined than the minimum temperature limit. The waters of Biscayne Bay exceeded the upper temperature breeding limit for several months each year, but rarely and only for short periods did the temperature drop below the lower breeding limit.

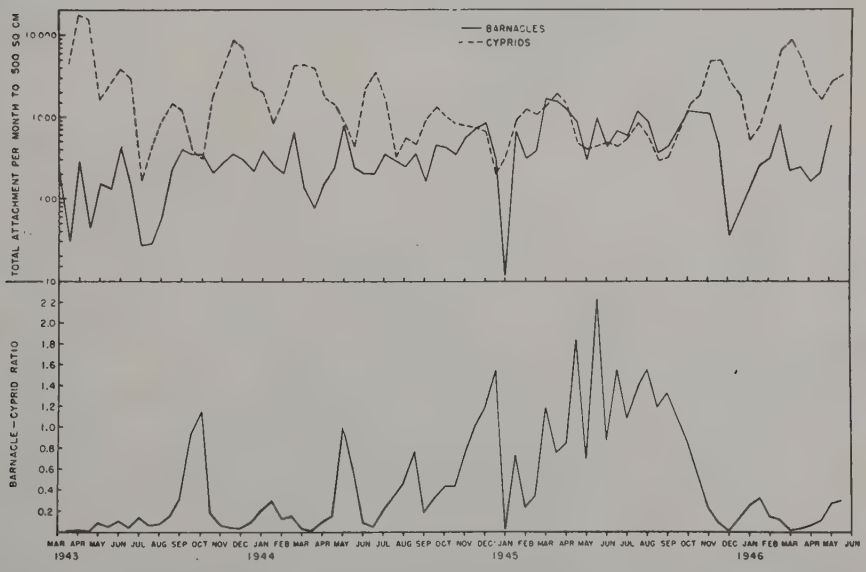

FIGURE 4. The monthly totals of daily cyprid settling and the monthly barnacle attachments on glass surfaces (500 sq. cm.), upper half. The ratio of barnacles to cyprids attached in each monthly period, lower half.

The numbers of barnacles found on the monthly collectors showed considerable variation, as indicated in Figure 4. For the entire period of observation the monthly barnacle collections dropped below 100 only eight times and went above 1000 only six times. The extreme numbers of barnacles collected in one month were 10 in December 1944 and 1615 in February 1945. However, extreme fluctuations in numbers of barnacles did not usually occur in two successive collections but followed a period in which a trend of rising or falling numbers was evident. Although not as marked, a rising trend in the monthly collections of barnacles during the period of 1943–1945 was observed, reaching a peak simultaneously with the low point of the monthly totals of cyprids.

Of the varying numbers of cyprids attaching daily it was assumed that all or some portion metamorphosed and grew to adult size. For comparison with the monthly barnacle collections the daily cyprid attachments were totaled every 15 days for the preceding 30-day period. The monthly cyprid totals, in general, showed a greater fluctuation than the monthly barnacle collections, as indicated in Figure 4. During the 38 months of observation, the numbers of cyprids attaching in a month decreased to a minimum in 1945 and then rose once more. This fluctuation is more clearly indicated in Table II, in which the number of monthly

TABLE II

Number of monthly cyprid totals greater and less than 1000 in six-month periods

Period	>1000	<1000
March 15, 1943–September 1, 1943	9	3
September 15, 1943–March 1, 1944	9	3
March 15, 1944–September 1, 1944	6	6
September 15, 1944–March 1, 1945	4	8
March 15, 1945–September 1, 1945	2	10
September 15, 1945–March 1, 1946	9	3

cyprid totals greater than 1000 are compared with the number of monthly totals less than 1000 for six-month periods. The number of monthly cyprid totals of less than 1000 reached a maximum in the period from March 15, 1945 to September 1, 1945. The concurrence of a high proportion of monthly cyprid totals less than 1000 with a period of maximum barnacle collections suggests that conditions for survival and maturity of the cyprid were optimum when the daily rate of attachment totaled 400 to 1000 per month (Fig. 4, upper half).

However, there were five occasions when the monthly cyprid totals in this range were not paralleled by monthly barnacle collections indicative of good survival. Since three of these collections were in the summer and two in the winter, it was not possible to identify these anomalies with a particular temperature condition or any other specific phenomenon. Cyprid totals of 2000 or more, which were found in 25 out of 74 monthly summations, invariably resulted in high mortality and poor survival. These data have been graphically presented by Deevey (1947) in a recent review of natural populations of animals. The phenomenon of attachment of enormous numbers of cyprids and high mortality was attributed by Moore (1935) to depletion of the stock of food in the water by the extra-large pop-

ulation. It should be pointed out that there were several occasions, particularly in 1945, when monthly cyprid totals slightly greater than 1000 were paralleled by large barnacle collections.

The ratio of the monthly totals of barnacles to cyprids is presented in the lower half of Figure 4. As shown, a ratio of 1 indicates survival of all attaching cyprids, and values less than 1 indicate the degree of survival (and mortality) of the cyprid population. In addition, there is the anomalous condition of ratios greater than 1, which indicates more adult barnacles at the end of a month than the total of settling cyprids in the same period.

The survival ratio was greater than 1 in October 1943, May and December 1944, and on nine of the monthly collections in 1945. A satisfactory explanation of this unusual condition may be found in the thesis of Phelps (1942) and of Scheer (1945) that the bacterial slime film, which forms on surfaces submerged in the sea, provides an environmental condition more suitable for attachment and growth than a clear bare surface. The daily collector, wiped clean every morning, may not have been as attractive a surface for attachment as the collector continuously immersed, which permitted a slime film to form within a few days after immersion.

During the period of observation, a distinct tendency toward greater survival of the cyprids was observed, reaching a peak in 1945 and then decreasing sharply. Although occasional rises of the barnacle-cyprid ratio were indicative of good survival in 1943 and 1944, the year 1945 was by far the best survival year.

Another factor limiting the survival of barnacles was the area available for growth on the collecting surface. The maximum adult population, one month old, was obtained during February 1945 when 1615 barnacles filled the collector. On many other occasions, particularly during the summer months when the growth rate was highest (Weiss, 1948), considerably fewer barnacles, for example 525 in June 1945, filled the same collecting area. Thus the area available for barnacle attachment was limited by the rate of growth of the barnacles initially attached.

Summary

1. The daily barnacle cyprid attachment in Biscayne Bay, Florida, and concomitant water temperature and salinity measurements were recorded continuously during a period of 38 months.

2. No relationship between the frequent peaks in cyprid settling and changes in temperature and salinity was established.

3. Seasonal periods of heavy cyprid attachment were observed to occur within a temperature range from 18° C. to 27° C.

4. The survival of cyprids increased gradually from 1943 to 1945 and then decreased sharply, as shown by a comparison of monthly barnacle collections with monthly totals of daily cyprid attachments.

5. Seasonal variation in growth rates was observed to be an important factor in limiting the numbers of barnacles attached per unit area.

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Contribution No. 439

Reprinted from JOURNAL OF METEOROLOGY, Vol. 5, No. 4, August, 1948, pp. 161–164
Printed in U. S. A.

DROP SIZE, INTENSITY, AND RADAR ECHO OF RAIN

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(Manuscript received 31 January 1948)

ABSTRACT

The various experimental relations between radar echo, intensity, and rainfall rate are examined utilizing a simple relation between terminal speed and size of raindrops and an empirical drop-size distribution. The drop-size law is such that the fraction of total rain volume of different drop sizes in the air is found to be normally distributed with respect to the fall speed relative to that of the median size drop.

The relation between the size of raindrops and rain intensity has been mentioned on numerous occasions, particularly recently by Laws and Parsons (1943) and in connection with radar echo by Marshall, Langille, and Palmer (1947).

A simple relationship relating drop size, intensity, and radar echo may be derived. In a single storm these factors depend on all drop sizes. Consider drops of diameter between $D - \frac{1}{2}\delta D$ and $D + \frac{1}{2}\delta D$. Then the radar echo is proportional to ND^6 where $N\delta D$ is the number of drops between the diameter limits, in unit volume of air[2] (Wexler and Swingle, 1947; Marshall *et al.*, 1947). N is then the number of drops per unit volume per diameter interval.

Terminal velocity of drops

The terminal velocity, v, of a drop is attained when the gravitational force on it is balanced by the drag of the air through which it is falling:

$$\tfrac{1}{6}\pi D^3 \rho_w g = \tfrac{1}{4} C_d \pi D^2 \rho v^2,$$

where ρ_w is the density of water, g is the acceleration of gravity, C_d is the drag coefficient of a spherical drop, and ρ is the density of air. Thus,

$$v^2 = K^2 D, \tag{1}$$

where $K^2 = \frac{2}{3}\rho_w g/\rho C_d$. Laws (1941) values of terminal fall-velocity are plotted in fig. 1, together with the theoretical relation (1). This relation is seen to hold up to a diameter of 0.4 cm after which the deformation becomes great enough to cause the terminal velocity to remain substantially constant (Spilhaus, 1948). From fig. 1, K has a value of 1.42×10^3 cm$^{\frac{1}{2}}$ sec^{-1}.

The contribution (R_D) of drops of each size to the rainfall intensity is the volume of water of all drops of this size falling on a horizontal area in unit time, expressed as a depth of water over the area. This is equal to the volume of water corresponding to drops of diameter D in a unit volume of air times the velocity of fall of these drops:

$$R_D = \tfrac{1}{6}\pi N D^3 v = kND^{7/2}, \tag{2}$$

where

$$k = \tfrac{1}{6}\pi K = 0.745 \times 10^3 \text{ cm}^{\frac{1}{2}} \text{ sec}^{-1}.$$

Drop-size distribution

Now, as the drops are not of uniform size, some description of the drop-size distribution must be introduced to derive the relation between the total radar echo $Z = \Sigma N D^6 \delta D$ and the total rainfall $R = \Sigma R_D \delta D$.

Laws and Parsons (1943) gives smoothed experimentally determined values of the distribution of the percentage volume of total rainfall on a horizontal surface, $R_D \delta D/R$, by diameter classes (δD). It has been found by the writer that a general size-distribution function exists for all rains from Laws' data. This drop-size distribution is given by the expression

$$\ln \frac{\bar{D} R_D}{R} = -k_0^2 u^2, \tag{3}$$

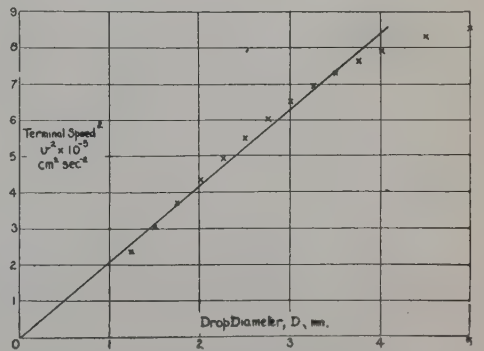

FIG. 1. Relation of terminal speed of fall to diameter of raindrops. The crosses are measurements by Laws (1941). The full line represents the theoretical relation $v^2 = K^2 D$.

[1] Woods Hole Oceanographic Institution Contribution No. 439.
[2] J. W. Ryde, Echo intensities and attenuations due to clouds, rain, hail, sand and dust storms at centimetre wavelengths. Research Laboratories of the General Electric Company, Ltd., England, Report No. 7831, 1941 (unpublished).

where $\bar{D}$ is the median diameter dividing rain falling on a horizontal surface into equal halves by volume, k_0^2 is constant for all rains, and $u = (D/\bar{D})^{\frac{1}{2}} - 1$. Equation (3) determines the drop-size distribution since R_D may be expressed in terms of N and D from equation (2).

Values of $\bar{D}R_D/R$ and u^2 were computed from Laws' and Parsons' (1943) measured (smoothed) results (their extrapolations were omitted), and in fig. 2, $\ln \bar{D}R_D/R$ is plotted against u^2 showing that the linear relationship (3) holds very closely for $k_0^2 = 11.5$, although there is a slight systematic deviation.

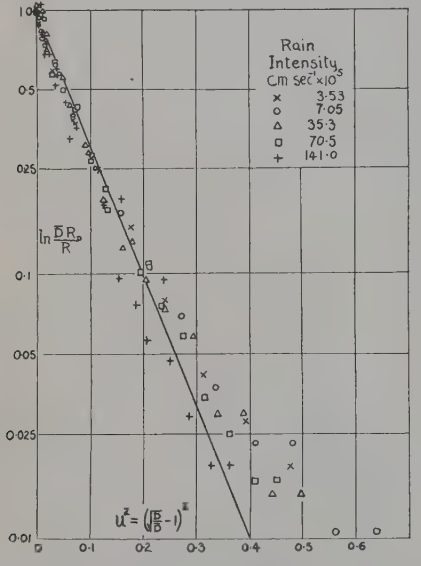

FIG. 2. Drop-size distribution in natural rain. Plotted points obtained from measurements of Laws and Parsons (1943). The full line represents the relation $\ln (\bar{D}R_D/R) = -k_0^2u^2$, with $k_0^2 = 11.5$.

These results indicate that a rain may be completely described by the median diameter of the drops and the rainfall intensity.

From the drop-size distribution law (3) combined with (2),

$$ND^{7/2} = k^{-1}R\bar{D}^{-1}e^{-k_0^2u^2}. \tag{4}$$

If the total radar echo $Z = \Sigma ND^6\delta D$ is expressed as an integral,[3]

$$Z = \int_0^\infty ND^6\delta D,$$

then it follows from the preceding equation that

$$Z = k^{-1}R\bar{D}^{-1}\int_0^\infty D^{5/2}e^{-k_0^2u^2}\delta D,$$

or, since $D = \bar{D}(u+1)^2$,

$$Z = 2k^{-1}R\bar{D}^{5/2}I_6, \tag{5}$$

where

$$I_n \equiv \int_{-1}^\infty (u+1)^n e^{-k_0^2u^2}\delta u$$

can be expressed ultimately in terms of

$$I_0 = \int_{-1}^\infty e^{-k_0^2u^2}\delta u,$$

through integration by parts.

For the total rain $R = \Sigma R_D\delta D$ we have from (2),

$$R = k\Sigma ND^{7/2}\delta D = k\bar{N}\bar{D}^{7/2}, \tag{6}$$

where $\bar{N}$ is the number of drops giving the same total rainfall intensity with the median drop diameter $\bar{D}$ as the actual rain. Eliminating $\bar{D}$ between equations (5) and (6), we obtain

$$Z = (2k^{-12/7}I_6\bar{N}^{-5/7})R^{12/7}. \tag{7}$$

From experiment, Marshall and collaborators (1947) give the empirical relation

$$Z = 190\ R^{1.72},$$

where Z is in $mm^6\ m^{-3}$, and R is the total rain in $mm\ hr^{-1}$. If this expression is transformed to cgs units (Z in $cm^6\ cm^{-3}$, R in $cm\ sec^{-1}$) and our exponent 12/7 used instead of 1.72, then

$$Z = 1.24 \times 10^{-2}R^{12/7}. \tag{8}$$

Evaluation of I_6 with $k_0^2 = 11.5$ and comparison of (7) with the empirical equation (8) yields the median number $\bar{N} = 1.7 \times 10^{-4}$ which is implied by (8) to be constant in all rains. It is to be expected that $\bar{N}$ would vary with $\bar{D}$; evidently this value is an average for the values of $\bar{D}$ found in the experimental tests.

To test the consistency of the value of $\bar{N}$ we may use an independently determined empirical relationship of Marshall and collaborators (1947):

$$M \equiv \tfrac{1}{6}\pi\rho_w\Sigma ND^3\delta D = 80\ R^{0.83},$$

where M (the total mass of rain in a unit volume of air) is in $mg\ m^{-3}$ and R in $mm\ hr^{-1}$. If this relation is transformed to cgs units and if we write $\frac{1}{6}\pi V$ for the total *volume* of rain in a unit volume of air,

$$V \equiv \Sigma ND^3\delta D = 1.24 \times 10^{-3}R^{0.83} \tag{9}$$

(V in $cm^3\ cm^{-3}$, R in $cm\ sec^{-1}$). If V is replaced by an integral, then it follows from (4) that

$$V = k^{-1}R\bar{D}^{-1}\int_0^\infty D^{-\frac{1}{2}}e^{-k_0^2u^2}\delta D,$$

or using the notation employed in (5),

$$V = 2k^{-1}R\bar{D}^{-\frac{1}{2}}I_0. \tag{10}$$

[3] The limits are taken from 0 to ∞ for simplicity, with no great error because in normal rains the number of drops approaching maximum size (about 7 mm) is negligible and the contribution of drops less than "raindrop" size (0.5 mm) is likewise negligible.

From (6) we have $\bar{D}^{-\frac{1}{2}} = k^{1/7}\bar{N}^{1/7}R^{-1/7}$; hence (10) becomes

$$V = (2k^{-6/7}\bar{N}^{1/7}I_0)R^{6/7}.$$

Using the value of $\bar{N}$ previously obtained,

$$V \equiv \Sigma ND^3\delta D = 1.00 \times 10^{-3}R^{6/7},$$

which is to be compared with (9). If the empirical relation in (9) were worked up using our exponent 6/7 instead of 0.83 the coefficient would be reduced by about 10 per cent and shows good agreement with our value.

Physical meaning of the drop-size distribution law

The drop-size distribution law may be integrated in the following fashion:

If R is eliminated between equations (4) and (10), we find

$$ND^{7/2} = \tfrac{1}{2}VI_0^{-1}\bar{D}^{-\frac{1}{2}}e^{-k_0^2u^2},$$

where $V \equiv \Sigma ND^3\delta D$, apart from a factor $\frac{1}{6}\pi$, is the total volume of rain in unit volume of air. Since $\delta D = 2(D\bar{D})^{\frac{1}{2}}\delta u$, the preceding equation may be written

$$\frac{ND^3\delta D}{\Sigma ND^3\delta D} = I_0^{-1}e^{-k_0^2u^2}\delta u.$$

If I_0 is evaluated using the value of k_0 from fig. 2 it is found to equal very closely $\sqrt{\pi}/k_0$; therefore

$$\frac{ND^3\delta D}{\Sigma ND^3\delta D} \equiv \frac{V_u}{V} = \frac{k_0}{\sqrt{\pi}}\,e^{-k_0^2u^2}\delta u. \qquad (11)$$

In the function $u = (D/\bar{D})^{\frac{1}{2}} - 1$, if $v = KD^{\frac{1}{2}}$ is substituted from (1), and if we set $\bar{v} = K\bar{D}^{\frac{1}{2}}$ as a median fall speed, corresponding to the median-sized drop, then

$$u = \frac{v - \bar{v}}{\bar{v}}.$$

Thus, u is the deviation of the fall speed of any drop from the fall speed of the median-sized drop, expressed as a ratio to the fall speed of the median-sized drop.

Coalescence of drops of raindrop size depends on collision, the frequency of which in turn depends on relative speed. It is therefore not physically unreasonable that the expression (11) corresponds to a distribution such that the proportion by water volume of drops per volume of air shows a normal variation with the function u of the speed relative to that of the drop of median diameter.

Referring to fig. 1, the substitution of $v = KD^{\frac{1}{2}}$ is valid for all but the unusually large drops over 0.4 cm diameter. The validity of this substitution would not affect (11) if the original data were classed by intervals of speed of fall.

Relation of $\bar{N}$ to $\bar{D}$

To describe the rainfall completely by a single measurement it is necessary, in addition to the distribution function (3) to know $\bar{N}$ as a function of $\bar{D}$, or to assume an average value as was done in the analysis of the empirical data of Marshall and collaborators.

Now Laws and Parsons (1943, fig. 1) give a relation between median drop diameter and rain intensity:

$$\bar{D} = 2.23\,R^{0.182},$$

where $\bar{D}$ is in mm and R in inches per hour. If this is transformed to cgs units and the exponent 0.182 replaced by 2/11,

$$R = 2.7\bar{D}^{11/2}.$$

Substituting this expression for R into equation (6), then

$$\bar{N} = 2.7k^{-1}\bar{D}^2 = 3.63 \times 10^{-3}\bar{D}^2. \qquad (12)$$

The data given by Smith and Fletcher (1947) on total number of drops also show a variation with the square of the median diameter.

On the other hand it is interesting to note that if Lenard's (1904) data on the number of drops falling on unit area in unit time, N_H, is converted to the number of drops in unit volume of air above the ground, by the relation $N = N_H/v$, it is found that the number of drops is about 5×10^{-4}, except for rains which he reported as stopping or starting, or short, sharp showers (see table 1). It is not expected that rains which are stopping or starting would follow any general drop-distribution pattern.

TABLE 1. Total number of drops and corresponding rainfall intensity for different types of rain; from data by Lenard (1904).

Number of drops $\times 10^6$ per cm^3	Comments	Rainfall intensity $R \times 10^4$ cm sec^{-1}
428	general rain looking very ordinary	1.50
605	general rain looking very ordinary	1.00
109	rain with breaks during which the sun shone	1.83
119	beginning of a short fall	0.84
81	sudden rain from a small cloud	5.34
472	violent rain	12.00
475	period of a heavy continuous fall	9.50
508	period of a less heavy continuous fall.	5.65
97	stopping of a continuous fall	4.34

Lenard's results showing $\bar{D}$ versus R are also plotted by Laws and Parsons (1943, fig. 1) and a relation of $\bar{D}$ proportional to $R^{2/7}$ fits fairly well, which, by similar reasoning as was used to obtain expression (12), implies that $\bar{N}$ is independent of $\bar{D}$.

After this manuscript was originally submitted, Wexler (1948) has summarized and examined the various empirical relations relating radar echo to rain intensity and gives the following expressions, where $Z = \Sigma N D^6 \delta D$ is in mm^6 m^{-3} and R in mm hr^{-1}.

TABLE 2. Summary of empirical relations between radar echo (Z) and rain intensity (R), as given by Wexler (1948).

Authority	Date	Place	$Z =$
Laws and Parsons	1943	U. S.	$320\ R^{1.44}$
Marshall and Palmer	1948*	Canada	$220\ R^{1.60}$
Anderson and collaborators	1947	Hawaii	$208\ R^{1.53}$
Best	1947	England	$224\ R^{1.54}$
			$630\ R^{1.45}$

* Revised computation for the same data upon which equation (8) was based.

Apart from the constant obtained by Best (for relatively few storms), there is fair agreement between these various expressions. Utilizing a relation $\bar{N} = C\bar{D}$, and eliminating $\bar{N}$ between equation (6) and (7), we obtain

$$Z = (2k^{-1.55}C^{-0.55}I_6)R^{1.55}.$$

The relation of $\bar{N}$ proportioned to $\bar{D}$ seems best to fit the various empirical relations.

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Contribution No. 440

THE SEA SAMPLER[1]

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INTRODUCTION

The original sea sampler, as described by Spilhaus (1940), consisted of six bottles, each built somewhat like a small version of a standard Nansen bottle. These surrounded a cylinder containing a releasing block which was operated by an ordinary bathythermograph pressure element. The tripping block, which was moved by the pressure element, was scored and grooved to accommodate a series of triggers, one for each bottle, which closed the stop-cocks in turn as the whole instrument reached predetermined pressures. The tripping block was arranged so that the triggering points of the different bottles could be varied at will. The instrument was designed for use with the bathythermograph, which was described earlier (Spilhaus, 1938 and 1940), and therefore the next step was to combine the two instruments so that a single pressure assembly operated the tripping block for the sea sampler and carried the slides for the record of the bathythermograph temperature.

Extensive observations with the combined thermographic sea sampler were made during the summer of 1940 and are described by Spilhaus (1941). This series of observations, designed to demonstrate the rapid measuring technique made possible by this instrument, provided 200 soundings, giving 200 temperature-depth curves and 1,400 salinity and oxygen values, all obtained in a continuous period of three and a half days. This represents an average of one sounding (giving temperature against depth, and seven oxygen and salinity values) every twenty-two and one-half minutes, or every two miles at the speed of the vessel utilized, which was 5½ knots. During World War II, and because of its immediate application to the operating problems of underwater sound, considerable refinement of the bathythermograph was made by Dr. Ewing and his associates at the Woods

[1] Contribution No. 440 from the Woods Hole Oceanographic Institution.

[2] The construction and testing was done in the course of work by the Woods Hole Oceanographic Institution under contract with the Office of Naval Research.

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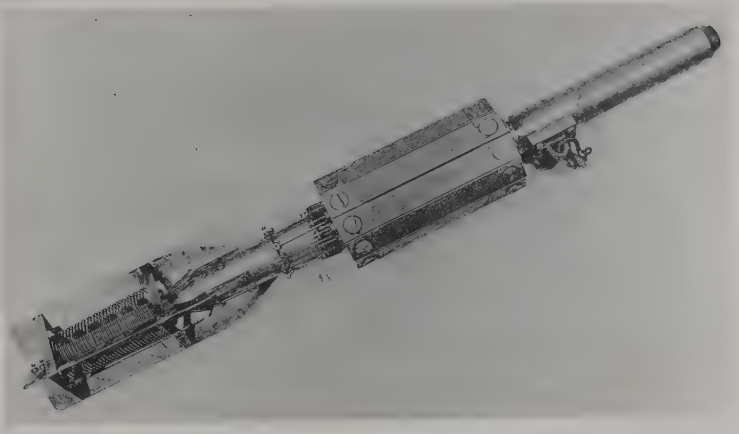

Figure 1. The new thermographic sea sampler.

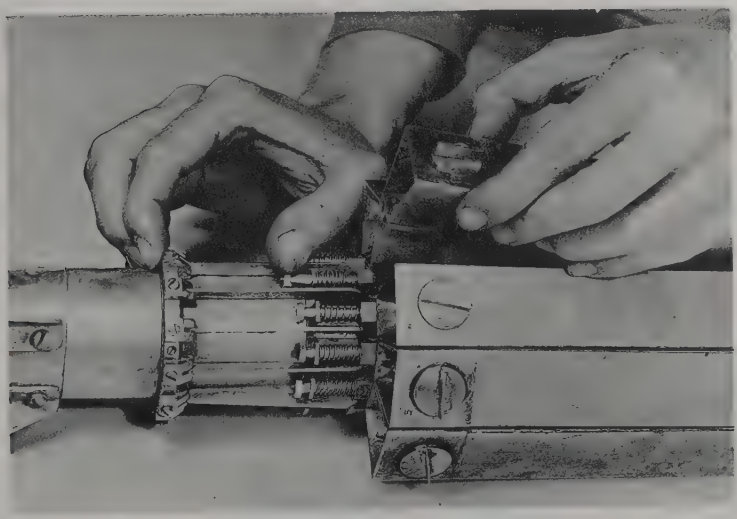

Figure 2. The sampler bottles showing method of removal.

Hole Oceanographic Institution, but improvement of the sea sampler was deferred until last year when the work described below was started.

DESCRIPTION OF THE NEW THERMOGRAPHIC SEA SAMPLER

In principle, the present instrument differs little from the thermographic sea sampler described earlier. However, two important improvements have been made. These are, first, streamlining the bottles so that the whole instrument may be used with the vessel underway at higher speeds, and second, arranging the tripping mechanism so that the samples are taken on the way up from the lowest depth reached rather than on the way down, as was the case in the earlier instrument. The number of bottles is increased to twelve, and the whole design is so arranged that in one or two minutes all the bottles and triggers can be removed without the use of any tools; the instrument is then identical to an ordinary bathythermograph and may be used as such.

STREAMLINING

So that this addition to the bathythermograph would give as little drag as possible, the bottles, twelve in number, were made in a trapezoidal shape and were fitted around the instrument to form a smooth cylinder of not much greater diameter than the width of the fins on the bathythermograph (Figs. 1, 2 and 3). Furthermore, to maintain the smooth exterior of the cylinder, the connecting bar and spring, which are necessary on each bottle to effect the simultaneous closing of the two rotary stop-cocks, were placed on the inside surface of the bottle; that is, on the side of the bottle that faces the bathythermograph

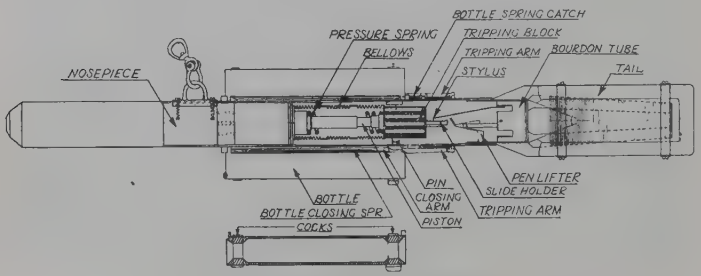

Figure 3. Diagram of Sea Sampler

cylinder. This has the additional advantage that the mechanism is protected from damage. The result of this streamlining as it affects the rate of fall of the combined thermographic sea sampler is well illustrated in Fig. 4, which shows a comparison between the drop of a bathythermograph and that of the sea sampler (with six of the twelve bottles attached). These tests, which show that the sampler dropped as fast as the bathythermograph, were made at a speed of 8½ knots and therefore indicate that the former should be utilizable at as high speeds as the latter. In the tests made, it took longer to bring in the sea sampler than the bathythermograph, but this is merely a matter of the power of the winch.

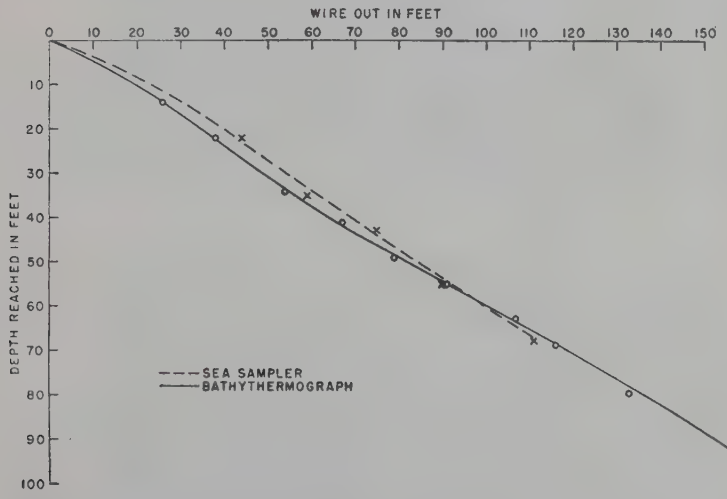

Figure 4. Comparison of the Rate of Drop of Sea Sampler and Bathythermograph with respect to Length of Wire Out while Underway at 8½ Knots

TRIPPING MECHANISM

The tripping mechanism is now designed so that water is trapped as the whole instrument ascends to the sea's surface. Thus the sample is never immersed in denser water, and more thorough washing of the bottle is accomplished. A further alteration is that the adjustment of the depth of tripping is now made by simple exchange of the tripping bars on the exterior of the instrument. In the earlier model these depths could be changed only by replaceable grooves in the tripping

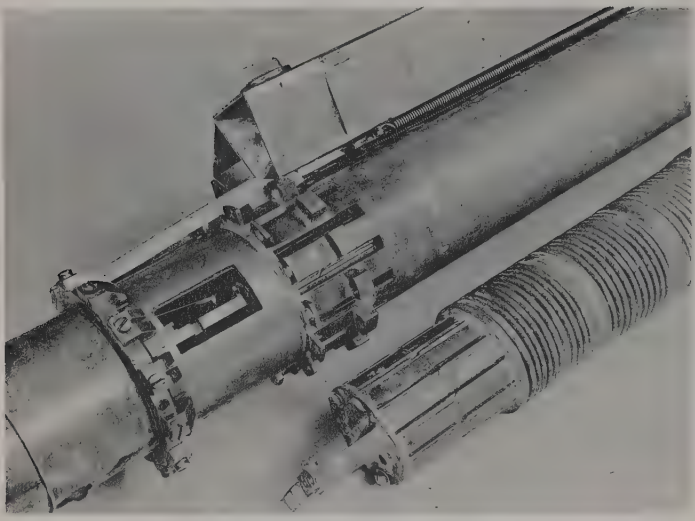

Figure 5. Tripping mechanism.

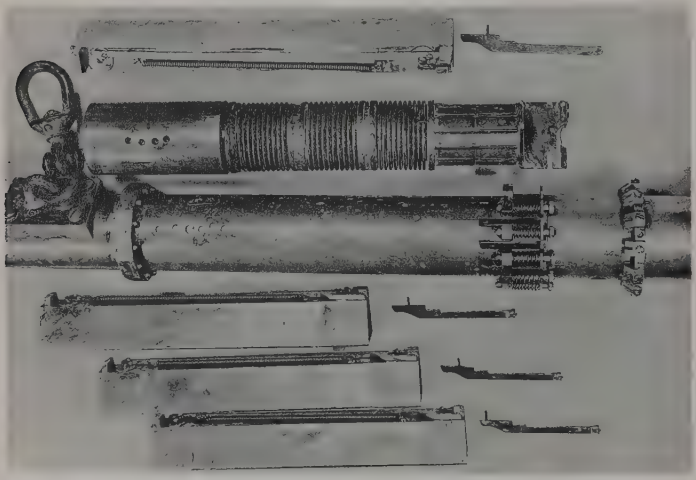

Figure 6. Sea sampler with bottles and triggers removed and a pressure unit carrying the tripping block.

block, which was inconvenient, since the pressure mechanism had to be withdrawn in order to do this. Figs. 5 and 6 and the diagram in Fig. 7 indicate the manner in which the tripping is achieved in the present instrument. Calibration of tripping depth can be carried out either in a pressure tank or by the use of an auxiliary device which withdraws the pressure element and then pushes it back into place,

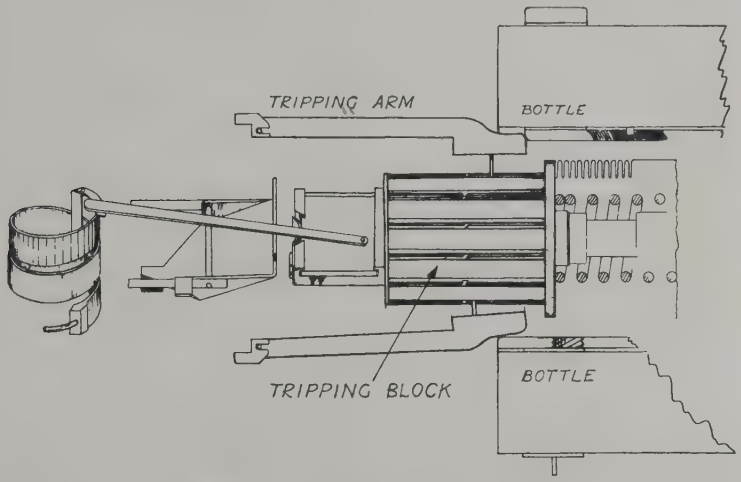

Figure 7. Diagram of Tripping Mechanism

thus simulating on the bench the compression of the sylphon and the spring due to water pressure. Fig. 8 shows calibration curves obtained by both methods. In this case, in order to show up any frictional errors to their maximum extent, a shallow pressure unit (120 feet) was utilized. Owing to the size of the pressure tank available, only three bottles could be used at one time in the tank tests. The method of test was to place the sea sampler in the tank, then build up the pressure until the deepest bottle was in a cocked position. The water pressure was then slowly decreased until a sharp crack, indicating the tripping point of the bottle, was heard. The pressure at this point was noted for each bottle and with each tripping bar. Repeated tests showed excellent consistency, any slight variation being attributable to the accuracy of reading the pressure scale. The bench tests were conducted in a similar manner, but, by withdrawing the pressure assembly and then pushing it back with the device described above. At the point of tripping, the stylus of the thermom-

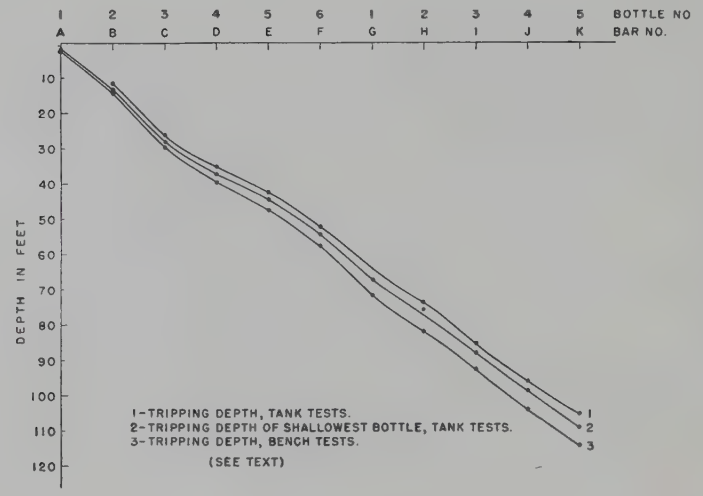

Figure 8. Calibration of Sea Sampler

eter was moved slightly on the smoked slide to mark the depth. It may be noted that the shallowest bottle in the group will trip two feet below its normal calibration. This is believed to be a frictional effect which may be minimized when all twelve bottles are in position around the instrument so that the sideways pressure of the tripping bars is evenly distributed rather than one-sided as in the case of these tests.

TRIALS AT SEA

Some tests of the thermographic sea sampler were made from the research vessel Balanus in order to compare salinities obtained by it with those obtained by the Nansen bottle technique. The purpose of these tests was twofold: first, to check the over-all performance of the sea sampler under conditions of practical use, and second, to study the effect of throttling, which prevents the complete interchange of water within the sampling bottles due to the constriction of the stop-cocks. The shallow bathythermograph pressure unit was used in order to magnify any frictional effect, and the station was chosen in the Narrows of New York Harbor, where an extreme salinity gradient was found. Under these conditions any errors due to the throttling of the stop-cocks of the sample bottles would be shown up by marked

differences of salinity between the sea sampler and the corresponding Nansen bottle. Test numbers 1, 2 and 3 (Table IA) were made at this

TABLE I. Salinities (‰) Obtained in Tests of the Sea Sampler and Nansen Bottles on Balanus Cruise B-19, March 25, 1948

A. Stations I, II and III at Anchor in Narrows, near Quarantine, New York (Lat. 40° 36.8′ N., Long. 74° 03.4′ W.)

Depth of Nansen Bottles and Tripping Points of Sea Sampler, m.	*I** 0950 hr.		*II** 1025 hr.		*III†* 1130 hr.	
	Nansen	*Sea Sampler*	*Nansen*	*Sea Sampler*	*Nansen*	*Sea Sampler*
1.2	10.91	12.85	9.56	10.95	10.21	10.86
4.0	11.51	16.51	10.14	14.42	10.72	10.99
7.6	17.38	——	15.12	22.65	——	——
9.8	22.03	23.82	21.37	24.83	——	——
13.7	23.84	25.77	25.95	——	——	——
16.2	25.61	26.47	26.78	——	——	——
Depth (max.) on B. T. (ft.)		77		78	55	68

B. Stations IV and V at Anchor, Middle of Sandy Hook Channel, New York Station VI Underway, Sandy Hook Channel (Lat. 40° 28.7′ N., Long. 74° 01.2 W.)

	*IV** 1325 hr.		*V** 1345 hr.		*VI‡* 1410 hr.	
1.2	14.51	14.87	14.63	15.12		——
4.0	15.17	15.81	14.97	15.81	None	14.76
7.6	15.82	16.04	15.86	16.06	Underway	15.91
9.8	16.09	——	15.97	16.11		——
13.7	16.20	——	16.02	17.79		——
16.2	16.94	——	17.07	——		——
Depth (max.) on B. T. (ft.)	55	65	55	67		70

B. T. 6 ft. below lowest Nansen Bottle. Vessel speed 8½ knots.

* Sea Sampler's vertical rate of ascent, 60 ft. in 10 sec.

† Sea Sampler brought up very slowly with stops.

‡ Sea Sampler's vertical rate of ascent, 60 ft. in 35 sec.

Temperature approximately 40° F. and homogeneous.

station in a depth of about 78 feet of water just off Quarantine. The salinities here were very low, ranging from about 9 ‰ at the surface to 27 ‰ at 50 feet. This gradient of salinity provided ideal and stringent conditions for tests on the throttling effect of the bottles. Numbers 1 and 2 were made by lowering Nansen bottles set at exactly the tripping depth of the six bottles used on the sea sampler. The

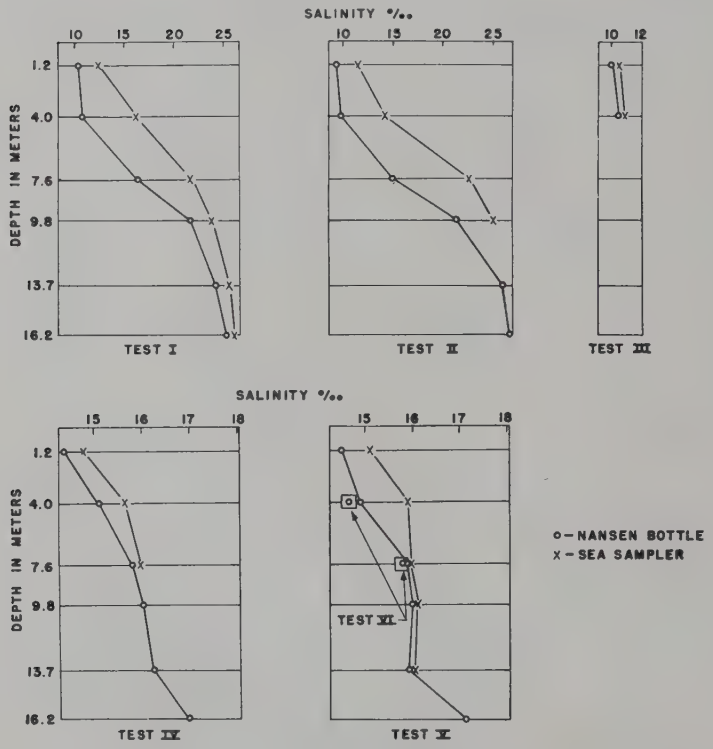

Figure 9. Tests of Sea Sampler Compared with Nansen Bottles

messenger was released to reverse the Nansen bottles at the same time as the sea sampler was withdrawn from the bottom.

In both these tests the sea sampler was brought up at the rate of about 60 feet in 10 seconds. Marked differences between the salinities were observed. These are shown in the curves in Fig. 9. The differences were systematic, however, and in the right sense to indicate that error was due to the throttling lag of the sampler bottles. Therefore, in test number 3 (Fig. 9), the sea sampler was brought up very slowly, with frequent stops to permit the complete interchange of water. It is immediately seen in this test that the differences between the Nansen bottles and the sea sampler are very materially reduced.

A further series, 4, 5, and 6 (Table IB), were made in about 70 feet of water just off Sandy Hook. Here the gradient of salinity was much less, varying from about 14½ °/₀₀ to 17 °/₀₀. Tests 4 and 5 were made with exactly the same procedure as tests 1 and 2. They show the same systematic excess of salinity obtained by the sea sampler over that of the corresponding Nansen bottle (Fig. 9). In this case, the difference is less because the gradient of salinity is less.

Immediately following test 5, the ship was put underway. As the test area was passed over at the speed of 8½ knots, the sea sampler was lowered for test 6. Here, the salinities obtained by the sea sampler were far closer to those of the Nansen bottles. This great reduction of the throttling error when the instrument is used underway is to be expected from two factors. First, in using the instrument underway, far more wire is played out to reach a particular depth; thus, in this case, it took 35 seconds to raise the instrument vertically through 60 feet of water compared to 10 seconds for the same depth at anchor. Second, with the vessel moving forward at the rate of 8½ knots, the relative velocity of the water through the bottles is much greater (even though the vertical speed of the bottle through the water is less than in a lowering made while hove to). These two factors both act to reduce the throttling error. The increased relative velocity of the water causes a greater rate of exchange in the bottle with time. The decreased vertical velocity of the bottle through the gradient causes a decreased rate of change of concentration with time, both factors tending to reduce the error. These effects are discussed quantitatively below.

THE LAG OF A SAMPLER DUE TO THROTTLING

In the pressure-operated sea sampler, a sample is taken by closing a container at a certain point as the whole instrument is moving through an environment with varying concentration of the constituent to be measured. In such a case there will be a certain error in the concentration determined from the entrapped sample due to imperfect exchange of the fluid through the container.

The diagram (Fig. 10) shows the arrangement of the cocks and the arrow shows the motion of the water relative to the sampler at a speed, v_r; then, if p_1 and p_2 are the pressures in front and at the back of the bottle respectively, the volume of water passing through the bottle in unit time is

$$Q = C_q\, a \sqrt{\frac{2(p_1 - p_2)}{\rho}},$$

where C_q is an orifice coefficient for the bottle, a is the area of the stop-

Figure 10. Diagram of Sampler Bottle

cock openings and ρ is the density of water. $p_1 - p_2$ will be proportional to the impact pressure of the water $= K\rho v_r^2/2$, where K is a constant less than unity due to any streamlining effect. Substituting,

$$Q = C_q\sqrt{K}\, a v_r .$$

Putting $C_q\sqrt{K} = k$, a constant for the instrument, the rate of mass flow into the container is

$$\frac{dM}{dt} = \rho k a v_r .$$

Let the concentration of the constituent be $C = M_s/M$, where M_s is the mass of the constituent and M is the mass of water. In an interval of time dt, suppose the sampler moves up a distance $-dz$, where the concentration in the environment has changed from C to $C - dC$. Then, if the concentration in the container was originally C_i, and complete mixing inside is assumed, an amount of water dM with this concentration has flowed out, and has been replaced by a similar amount dM with concentration

$$\frac{C + (C - dC)}{2} = C - \frac{dC}{2} .$$

The concentration in the container, assuming complete mixing[3], is then

$$C_i + dC_i = \frac{(M - dM)C_i + (C - dC/2)\, dM}{M}$$

$$dC_i = -\frac{(C_i - C)}{M}\, dM ,$$

so that the rate of change of concentration inside is then

$$\frac{dC_i}{dt} = -\frac{(C_i - C)}{M}\frac{dM}{dt} = -(C_i - C)\frac{V_r}{\xi} ,$$

[3] If *no* mixing is assumed, the rate of change of concentration inside is doubled, and hence all errors due to throttling are halved.

where $M = \rho V$ and $ka/V = 1/\xi$, which is a characteristic of the sampler bottle on the instrument.

Suppose, first, that the sampler is being raised through water which has a concentration C_o, constant for a considerable depth (so that the water in the container may be assumed also to be C_o). Further, that upon reaching a certain point, there is a sudden discontinuity of concentration which drops to C and remains constant with further decrease of depth. Integrating the equation for the rate of change of concentration in the container, we obtain

$$\frac{C_i - C}{C_o - C} = e^{-v_r t/\xi} ,$$

if t is counted zero at the discontinuity. ξ/v_r is the lag coefficient of the sampler in units of time, similar to the lag coefficient of a thermometer (see for example Middleton, 1941: 56–58). ξ/v_r represents the time for the difference of concentration in the container C_i, and in the environment C, to reduce itself to $1/\epsilon$ of its original value.

When the concentration varies with depth z, measured positive downwards with a gradient $\alpha = dc/dz$, then, if the whole sampler is moving upward at a rate $v_v = -dz/dt$, the concentration changes at a rate

$$\frac{dc}{dt} = - v_v \alpha .$$

Then

$$C = C_o - V_v \alpha t,$$

where C_o is the concentration at some lower point from which t is counted zero. The rate of change of concentration in the container is then

$$\frac{dC_i}{(C_i - C_o + v_v \alpha t)} = - \frac{v_r}{\xi} dt ,$$

or

$$\frac{dC_i}{dt} = - \frac{V_r}{\xi} \left[C_i - (C_o - v_v \alpha t) \right],$$

and

$$C_i - C = - \xi \alpha \left(\frac{v_v}{v_r} \right) \left(1 - e^{-v_r t/\xi} \right),$$

after $t >> \xi/v_r$

$$C_i - C = - \xi \alpha \left(\frac{v_v}{v_r} \right) = - \frac{V}{ka} \alpha \left(\frac{v_v}{v_r} \right).$$

If the sampler is being used from a vessel at anchor in no current, then $-v_v = v_r$,

and $$\frac{C_i - C}{\alpha} = \frac{V}{ak} = \xi .$$

If, however, it is being towed at a forward speed, then $-(v_v/v_r) = \cos\beta$, where β is the inclination of the path of the instrument to the vertical, or approximately the wire angle,[4] then

$$\frac{C_i - C}{\alpha} = \xi \cos\beta .$$

In a constant gradient of concentration, the indicated gradient, α_i, will equal the actual gradient α. Thus, the expression shows that if the characteristic ξ of the sampler is known, and if β is known, the indications may be corrected if necessary.

THE LAG COEFFICIENT AND "CHARACTERISTIC LENGTH" OF A SAMPLER

As the lag coefficient ξ/v_r of a sampler depends on the relative speed of the instrument to the water, it is more convenient to discuss lag in terms of ξ, which is a characteristic of the instrument alone. ξ has the dimensions of length. An ideal sample bottle with no obstruction to flow through it would have k = unity. Then $\xi = V/a$, and as the area a would be the area of cross section of the bottle for no obstruction, ξ would represent the actual length of this ideal bottle. In the case of real bottles with stop-cocks, k must always be less than unity, and it is then convenient to define ξ as the "equivalent length" of an ideal bottle. Equivalent length then is the length of a bottle with no throttling, which would have the same lag. If we assume that the tripping depth is at the depth of the top of the bottle, then in a steady gradient of salinity the actual sample in the bottle will always represent the salinity at the bottom of the equivalent ideal bottle. Thus

$$C_i = C + \alpha\xi \cos\beta \text{ (see Fig. 11).}$$

[4] β is only equal to the wire angle δ with the vertical, when the drag of the wire is considered negligible and when the speed of hauling in wire, v_w, is negligible compared to the forward speed of the vessel, v_f. In other cases, β is always larger than δ. If the assumption is made that the sea sampler lines up with the direction of the flow of water relative to it, then if the instrument has a drag equal to b times the square of the relative velocity v_r, and a weight W, it can be shown that $\cos\beta = b/w\, v_w v_f \cos\delta/\tan\delta$.

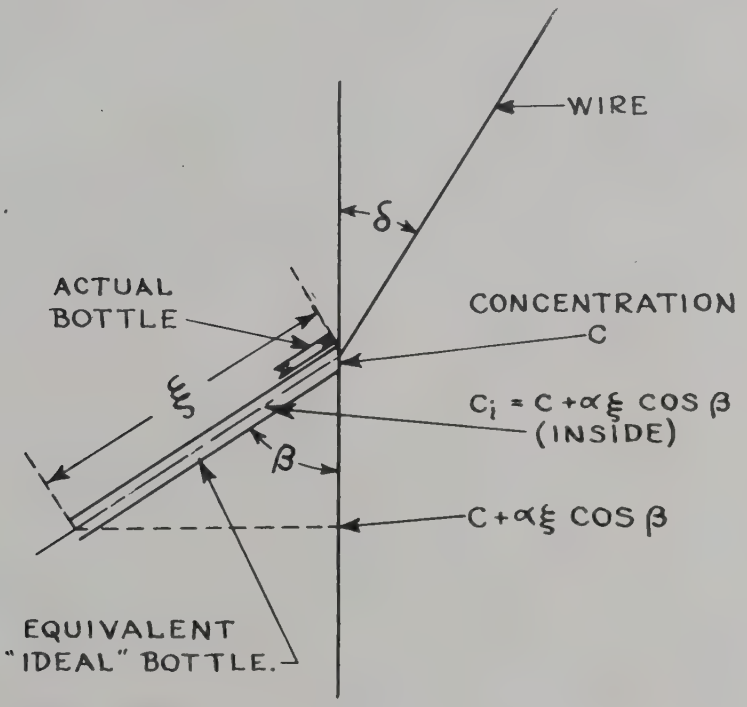

Figure 11. Equivalent Length of the Sampler Bottle in Relation to Lag in a Constant Gradient of Concentration

EXPERIMENTAL DETERMINATION OF THE EQUIVALENT LENGTH OF THE SEA SAMPLER

From tests 1, 2, 4 and 5, which were performed with the vessel stationary, $(C_i - C)/\alpha$ has an average value of about 2.5 m. (Fig. 9).[5] Therefore, 2.5 m. is the equivalent length of the present sea sampler. When used underway at 8½ knots, however, the inclination of the

[5] This value was computed in the following manner:

In tests 1 and 2 (Fig. 9) the gradient α was computed between the depths 9.8 m. and 4 m. where it is fairly constant. The error $(C_i - C)$ was measured at 4 m., assuming that there had been time enough to attain constant lag (5.8 m. $> \xi$). In the case of tests 4 and 5 (Fig. 9), the gradient between 7.6 m. and 1.2 m. and the error, at 1.2 m., were utilized. The value of the equivalent length from tests 4 and 5 agrees fairly well with that for tests 1 and 2, which were in different water.

bottle to the vertical is very great and the actual vertical distance between the top and bottom of the equivalent ideal bottle is reduced by the factor of the cosine of this inclination, so that the error due to throttling is reduced in this case to a very small fraction of the 2.5 m. which obtains for stationary operation.

Apart from the factor K in the expression $\xi = V/aC_q\sqrt{K}$, all the factors are easily determinable in the laboratory. C_q, determined by a discharge test at various heads of water through the sampler bottle totally immersed, was found to be about 0.57, $V = 120$ cm^3 and $a = 1.44$ cm^2. Using $\xi = 2.5 + 10^2$ cm gives $K = 0.34$. This means that the streamlining of the whole instrument is such that only about one-third of the full dynamic pressure on the bottle is effective in causing the interchange of water.

PRACTICAL USE OF SEA SAMPLER

An example of the use of the sea sampler was provided when Woods Hole Oceanographic Institution was requested to investigate a problem concerning the dispersal of acid waste as it was released from a barge. The BALANUS followed in the wake of the barge at various distances, and about 50 lowerings with the sampler were made; a vertical section was thereby constructed showing the concentration of the waste at various horizontal distances and depths from the point of efflux in the barge. It is cited as an example of an unusual type of operation that can be accomplished with the sea sampler which would hardly be possible by use of other existing means.

SUMMARY

An improved model of the thermographic sea sampler (a sea sampler combined with a conventional bathythermograph) is described. It consists of twelve sample bottles attached to a standard bathythermograph and arranged to trip at various pressures (depths) which can be chosen at will. Comparisons of samples taken in this manner with those obtained by the use of Nansen bottles are shown and a theory for the lag of a sampling device of this kind is given. Theory and observation indicate that the errors of the sea sampler are small when used underway. The theory further permits correction of observations for lag when necessary in terms of a single "characteristic length" of the instrument and the angle of inclination of its path through the water.

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Contribution No. 441

QUANTITATIVE STUDIES OF SUMMER PLANKTON POPULATIONS OF THE WESTERN NORTH ATLANTIC

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The following is an account of plankton measurements obtained during a cruise[2] of the research vessel "Atlantis" to the Mid-Atlantic Ridge between July and September 1947. It is primarily a study of plankton in the great central Atlantic eddy known as the Sargasso Sea. For comparative purposes, a small amount of material was obtained from New England coastal waters, the so-called slope water area lying off the edge of the Continental Shelf, and the Gulf Stream. An August cruise by the "Balanus" assisted in gathering this subsidiary data. The material to be described consists of phytoplankton assays by the plant pigment method of Harvey (1934), measurements of zooplankton collected by means of Clarke-Bumpus (1940) samplers, and experimental estimates of phytoplankton photosynthesis and zooplankton respiration. The plankton work was accompanied by physical and chemical measurements that will be mentioned briefly here and will be described more fully in another publication.

Before this cruise there has been little information available on the quantitative distribution of plankton in the Sargasso Sea in summer. Phytoplankton studies, consisting of cell counts (Lohmann, 1920) and pigment analyses (Riley, 1939), were available only for the May–June period. Zooplankton collections by Jesperson (1935), Leavitt (1935, 1938), and Clarke (1940) provided a fairly adequate picture of relative regional abundance, and the last author mentioned obtained enough tows at different times of the year to conclude that seasonal variations of zooplankton in the Sargasso Sea were small or nonexistent. However, all these collections were made by means of "standard" tows with unmetered nets, and the results were not readily convertible into strictly quantitative terms. It was therefore desirable to obtain a few measurements that would be more directly comparable with the

[1] Contribution No. 441 from the Woods Hole Oceanographic Institution.

[2] Jointly sponsored by the National Geographic Society, Columbia University, and the Woods Hole Oceanographic Institution.

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larger body of available information on the zooplankton of the New England coastal waters and offshore banks. In addition, a first attempt has been made to learn something of the organic content and metabolic requirements of the Sargasso Sea zooplankton.

THE PHYSICAL AND CHEMICAL ENVIRONMENT

Environmental data and plankton measurements are listed in the APPENDIX. The observations were obtained near the peak of the seasonal temperature progression, of which the annual range is about 10° C in the Sargasso Sea and 20° or more in the coastal water.

Nutrients were low everywhere in the surface waters. Some of the nitrate readings were lower than the best "nitrate-free" seawater blanks that could be obtained. Probably there is a seasonal diminution in nitrate in the Sargasso Sea, since previous analyses (mostly between January and June in the western part of the area) have yielded readily measurable values of 1 to 2 mg-at per m^3. Phosphate in the surface water was very slightly higher than most of the winter and spring determinations. However, one series of phosphates obtained in November and December 1931 (Seiwell, 1935) was of the order of 0.15 mg-at of P per m^3. Thus there is some slight evidence of seasonal changes in the nutrient concentration in Sargasso Sea surface waters, but they could hardly be more than a tenth or a twentieth of the seasonal variations in temperate waters.

Minimum concentrations of nutrients generally were found at depths of 25 m to 100 m rather than at the surface, suggesting a superior rate of phytoplankton production at subsurface levels and even implying that regeneration might exceed production in the immediate surface layer. This matter will be discussed more in detail later.

PHYTOPLANKTON

Plant pigment analyses were made by filtering one to four liters of water through fine filter paper, treating the residue with acetone, and comparing the acetone solution colorimetrically with the Harvey (1934) standard.

Fig. 15 shows the surface concentration of plant pigments at twenty stations. At five Sargasso Sea stations there were sufficient analyses at other depths to estimate the total phytoplankton crop in terms of Harvey units per m^2 of sea surface, and these figures are shown in parentheses immediately below the surface values.

Analyses of coastal water ranging from 4,000 to 18,000 Harvey units per m^3 are in accord with previous studies of coastal and offshore bank

waters during the summer season. The slope water value of 11,000 units is higher than previous summer records. It suggests that the sporadic summer flowerings often noted in the coastal zone are not entirely limited to inshore waters.

In the Sargasso Sea, the following averages were obtained for the depth distribution of plant pigments: surface, 140 units; 100 m, 220 units; 200 m, 120; and 300 m, 60. The mean total population measured 49,000 units per m² of sea surface. All averages were approximately one-sixth the mean values obtained in May 1939, the only other time the method had been used in this region. It remains to be

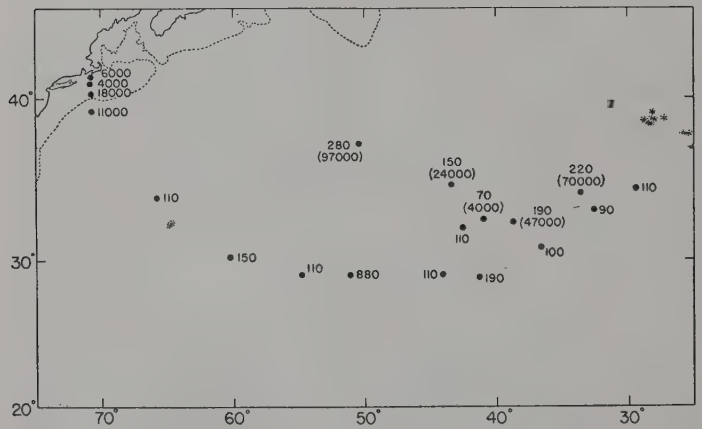

Figure 15. Phytoplankton pigment analyses. Surface concentration in Harvey units per m³; in parenthesis, total quantity in Harvey units per m² of sea surface.

seen whether this represents a normal seasonal trend or is indicative of atypical conditions at one time or the other. However, it is apparent that there was a decline during the period of the cruise, since the mean surface concentration was 180 units at stations before August 15 and 110 units after that date.

Experimental estimates of the photosynthesis of surface water phytoplankton were obtained by suspending light and dark bottles of surface water in a tub of water on deck for twenty-four hours and then measuring the differences in their oxygen content. The same method was previously used in studying a part of this area in May–June 1939 and in several cruises to Georges Bank, of which the ones in September

1939 and June 1940 are most nearly comparable from the seasonal standpoint with the present survey (cf. Riley, 1939, 1941).

Two coastal water stations of August 6 yielded values of 0.51 and 0.56 ml of oxygen produced per liter per day. These were higher than the mean (0.10) of two stations at nearly the same positions in early June 1939, but they fell within the general range of values (0.04 to 0.83 ml) obtained in the part of Georges Bank that lies between the 30 and 100 fm. curves.

A value of 0.19 ml per liter per day was found at the slope water station of August 7, as compared with a mean of 0.16 ml in two 1939 experiments and a range of 0.03 to 0.51 ml in the slope water south of Georges Bank.

Sixteen experiments in the Sargasso Sea between July 25 and September 10, 1947 ranged from −0.13 to 0.06, with a mean of −0.02. The average of previous work in May 1939 was 0.05 at five stations. It is unlikely that the mean of the recent data differs significantly from zero. However, there is little doubt that consumption exceeded production at the sea surface. The average surface water oxygen concentration was slightly undersaturated. The concentration increased between the surface and a depth of 25 m. Thus the surface content would tend to be increased both by interchange with the atmosphere and by vertical turbulence. Undersaturation could persist only under the circumstance that oxygen utilization *in situ* exceeded production.

Stations with analyses at depths of 1, 25, 50, and 100 m invariably showed an oxygen maximum at 50 m, both in absolute content and in percentage saturation (102 to 106%). At the depth of maximum concentration, which is conveniently called 50 m but might actually lie anywhere between 25 m and 100 m, vertical turbulence must continually tend to lower the oxygen concentration by mixing with undersaturated water from both greater and lesser depths. Therefore, the continued existence of a slight supersaturation at this intermediate depth must mean that oxygen production by photosynthesis exceeded the biologial utilization of oxygen.

Comparison of the Sargasso Sea stations made early in the cruise (4606, July 26; 4610, August 7) with later ones (4615, August 31, to 4617, September 4) shows no consistent trend, either seasonal or regional, in oxygen content. It therefore seems likely that a more or less steady state existed over a wide area in which the rate of increase of oxygen by phytoplankton production was approximately equal to the decrease that resulted from vertical turbulence. This can be written in the form of a simplified equation (for a more complete treatment of the problem see Sverdrup, 1938)

$$R = -\frac{A_z}{\rho} \cdot \frac{\partial^2 O}{\partial z^2}, \tag{1}$$

in which R is the net rate of production of oxygen by biological processes, A_z is the coefficient of vertical eddy diffusivity, ρ is the density of sea water, O is oxygen content, and z is depth. The vertical oxygen gradients and their change with depth can be estimated roughly from the oxygen determinations at 25, 50, and 100 m. The unknowns in the equation therefore are R and A_z. The latter can be determined by examining the change occurring during the same period in a conservative property such as temperature. The equation for the temperature change is

$$\frac{\partial \vartheta}{\partial t} = \frac{A_z}{\rho} \cdot \frac{\partial^2 \vartheta}{\partial z^2}, \tag{2}$$

in which t is time and ϑ is temperature.

TABLE I—Averages of Temperature, Oxygen, Phosphate, and Nitrate at Stations 4606, 4610, 4615, 4616, and 4617. Values Identified by (a) Are Averages of the First Two Stations, (b) the Last Three and (c) All Five

Depth in meters	25	50	100
Temperature (a)	24.8	22.0	19.5
Temperature (b)	28.0	—	20.9
Oxygen (c)	4.66	5.20	4.91
Phosphate (a)*	0.05	0.02	0.16
Phosphate (b)	0.020	0.023	0.047
Phosphate (c)	0.028	0.023	0.075
Nitrate (a)	1.95	0.40	1.15
Nitrate (b)	0.55	0.57	0.70
Nitrate (c)	1.11	0.52	0.88

* Data available only for station 4610.

Table I shows the basic data required for estimating production in the Sargasso Sea according to these equations. Phosphate and nitrate averages are included, since they will be used later for similar calculations.

The numerical approximation to equation (2) is

$$\frac{2.3}{2.77 \times 10^6} = \frac{A_z}{\rho} \cdot \frac{1}{37.5 \times 10^2} \left(\frac{-2.5}{50 \times 10^2} - \frac{-2.8}{25 \times 10^2} \right).$$

The mean temperature increase between groups (a) and (b) is 2.3°, and this divided by the difference in seconds between the median times of the two sets of observations is the time change in temperature. The temperature gradients are expressed as the difference between the 100 m and 50 m temperatures and the 50 m and 25 m ones, each divided by

the depth of the stratum in centimeters. The gradients must be expressed as the mean of stations 4606 and 4610, since 50 m temperatures were not obtained at the last three stations. The second derivative is the difference between the two gradients divided by the vertical distance between the midpoints of the two strata, namely 37.5 m. The numerical solution is $A_z/\rho = 0.19$ g per cm per second.

This figure can now be applied to equation (1) with the result that

$$R = \frac{-0.19}{37.5 \times 10^2}\left(\frac{-0.29}{50 \times 10^2} - \frac{0.54}{25 \times 10^2}\right) = 1.4 \times 10^{-8} \text{ ml of oxygen}$$

per liter per second.

The net daily oxygen production thus is estimated to have been 0.0012 ml per liter per day in the 25 m to 100 m stratum, equivalent to a carbohydrate carbon production of 0.64 mg per m^3 per day. Allowing what appears at present to be a normal phytoplankton carbon content of 17 mg per 1000 Harvey units of pigments, the estimated production represents a daily phytoplankton increase of 20% within the depth range specified. Since this depth range probably constituted nearly all of the stratum in which production exceeded consumption, it seems fair to estimate that the net total production was of the order of 48 mg of carbon per m^2 of sea surface per day, or about 6% of the total population.

No high degree of accuracy can be claimed for these results. In addition to the usual analytical and sampling errors, there is an error of unknown magnitude resulting from the exclusion of current transport and lateral mixing from the calculation. Nevertheless, in two respects the results seem reasonable. It will be shown later that the food requirements of the zooplankton appear to be slightly larger than the estimated plant production, and this is a necessary concomitant of the observation that the phytoplankton was decreasing slowly during the period of investigation. In the second place, the calculated production coefficient is of the same order of magnitude as the one previously estimated for the May 1939 data. At that time it was calculated from field experiments that photosynthetic activity produced about 4.2 g of carbon per m^2 per day, and phytoplankton respiration utilized perhaps 3.0 g. The difference of 1.2 g, or 450 mg of carbohydrate carbon per m^2 per day, which theoretically represents phytoplankton growth, is estimated to be equivalent to a growth coefficient of 8.5% of the total population per day.

Table I shows nitrate and phosphate minima at 50 m, or gradients increasing with depth. Both types of distribution are indicative of transport of these substances into the 25 m to 100 m stratum. The data are not entirely suitable for calculations of nutrient utilization according

to the principles of equation (1), since the gradients changed between the early and later part of the cruise. Therefore the existence of a steady state is questionable, and while the calculations are included for the sake of completeness, no attempt will be made to interpret their meaning.

Estimates based on the three sets of average gradients in Table I, (a), (b), and (c), show an apparent variation in both nitrate and phosphate utilization of greater than ten-fold magnitude. Thus, net phosphate consumption is found to range from 0.0005 mg of P per m^3 per day (b) to 0.0055 mg (a), and nitrate from 0.0035 mg of N per m^3 per day (b) to 0.047 mg (a). Even the largest estimates are smaller than would be required to give the phytoplankton a "normal" carbon : nitrogen : phosphorus ratio. Data by Fleming (1940) indicated an average C : N : P ratio in temperate water plankton of 41 : 7.2 : 1. The nearest approach to this that can be postulated with the present set of data is 130 : 8.5 : 1. It is fruitless to speculate on whether this implies actual nutrient deficiency in the Sargasso Sea phytoplankton or simply results from vagaries of the method.

ZOOPLANKTON

Zooplankton was collected by small, quantitative plankton samplers of the type described by Clarke and Bumpus (1940), which contain current meters to measure the volume of water strained. Oblique tows were made at approximately 2 knots for a half hour period, using nets of no. 10 silk. Usually two samplers were used at the same time, one with 0 to 400 m of wire out, the other from 400 m to 800 m of wire. In some cases only the upper sampler was used, or the lower one failed to open properly at depth. In coastal waters a single sampler was used, towing from the surface to as near the bottom as practicable.

The amount of water strained during a tow averaged about 8 m^3, with a total variation of 3 to 25 m^3. The smallest value was in coastal water where some clogging occurred. The largest was obtained from the deep sampler at a Gulf Stream station, where presumably the vertical current velocity pattern was such that the sampler towed faster than 2 kt. These are extreme cases, but they illustrate the difficulty of comparing so-called "standard" tows made with unmetered nets.

The Sargasso Sea collections generally had a volume of only a few tenths of a cubic centimeter, which was not considered adequate for volume measurements of the kind used by most previous investigators. It was desirable to use a method that would obtain greater accuracy with small samples and at the same time to maintain continuity with previous work. Therefore the samples were first prepared as for

measurements of displacement volume by draining thoroughly on a bolting silk filter after two washings with distilled water. The samples were then weighed. In a few cases where the quantity of material was sufficient for comparison of volume determinations with weights (1 to 14 cc), the volume in cubic centimeters did not differ by more than 10% from the wet weight in grams. After this the samples were dried and weighed, ignited, and weighed again. Thus the fundamental measurements obtained were wet weight (or volume) of plankton containing a small amount of trapped water, dry weight, an approximation of the weight of organic matter, and the weight of

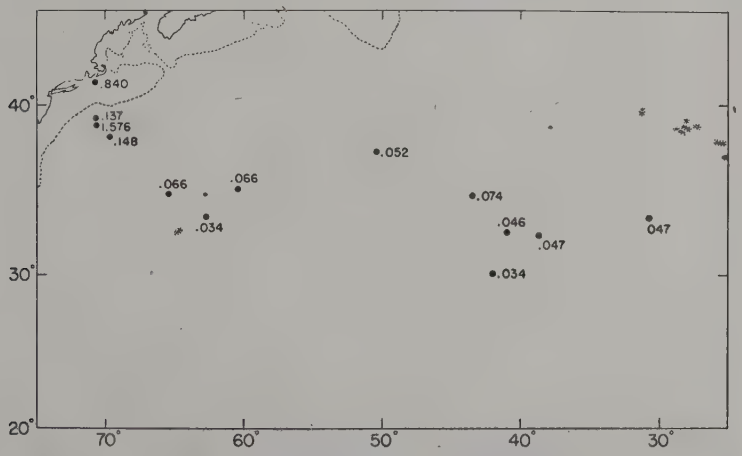

Figure 16. Zooplankton weight determinations. Wet weight in grams per m³; collections obtained by oblique tows in approximately the upper 400 m in deep water, and surface to near bottom in the coastal zone.

ash plus any sea salt that remained entrapped between the animals after the washing process. Clearly this is a compromise between the desire to obtain measurements comparable with the older work and the need for the development of more adequate quantitative methods.

Fig. 16 shows the distribution of zooplankton plotted as wet weight in grams per m³ of water in the upper stratum sampled. In most cases it is the average of slightly less than 400 m of water, the depth depending on the wire angle, but it also includes one slope water station where a single tow was made to 600 m, as well as a coastal water station where the total depth was 40 m, and the wire was let out 35 m.

The mean concentration in the nine Sargasso Sea hauls was 0.045 g per m³. The Gulf Stream station had a value about three times as high as the Sargasso Sea average. The two slope water stations had concentrations of 0.14 and 1.6 g per m³, respectively. Salps bulked large in the slope water collections. The nontunicate population was 0.025 and 0.035 g per m³, respectively. The coastal water station had a value of 0.84 g per m³, about the same as the mean of the slope water stations and nearly twenty times as much as in the Sargasso Sea.

Seven tows were made in the deeper stratum, with 400 m to 800 m

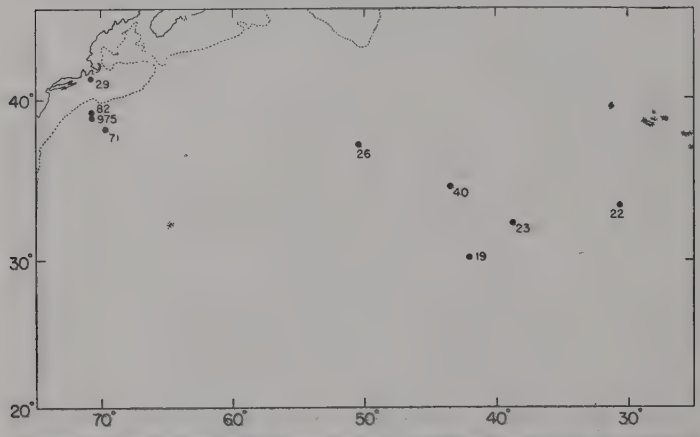

Figure 17. Zooplankton weight determinations. Rough estimate of the wet weight in grams of the total population underlying a m² of sea surface.

of wire out. Five collections in the Sargasso Sea ranged from 0.008 to 0.026 g per m³, with a mean of 0.014 g. The Gulf Stream station yielded 0.029 g per m³, and one tow in the slope water contained 0.861 g per m³. Thus in different parts of the region examined, the quantity of plankton in the deeper stratum was one-fifth to one-half the concentration nearer the surface.

The quantities that have been listed do not constitute the total zooplankton population, first because presumably some of the larger and more active animals can avoid capture by small nets, and second because Jesperson (1935) and Leavitt (1935, 1938) showed that in the slope water, in the Gulf Stream, and in the Sargasso Sea some plankton can be found to depths of 2,000 m or more. However, it was not practicable to attempt studies of the whole population, and the part

sampled is believed to be the most important from the standpoint of phytoplankton-zooplankton relations, which was the main object of the study. Therefore it seems worthwhile to examine the areal distribution of zooplankton (wet weight in g per m^2 of sea surface) obtained by the simple process of multiplying the mean concentrations by the depth towed. In this calculation the dubious correction for wire angle is not attempted in view of other errors that are unavoidable.

Fig. 17 shows the results. It is apparent that the total zooplankton was nearly the same in the coastal water and in the Sargasso Sea, while in the Gulf Stream and slope water it was considerably higher.

By way of comparison with previous work, Bigelow and Sears (1939) estimated that coastal water plankton in this area averages 0.5 to 0.8 cc per m^3. Clarke (1940) obtained an average of 0.54 cc per m^3 in 37 plankton sampler tows. He also made sampler tows in the slope water and Sargasso Sea, but the measurements were not listed in a way that permits precise comparison with present material. However, he described a series of scrim net hauls that yield an estimate of relative abundance. It was found that the mean annual ratio of plankton concentration in three areas—coastal water, slope water, and Sargasso Sea—was 16 : 4 : 1 for total zooplankton and 7 : 2.5 : 1 for the crustacean fraction.

These ratios and absolute values are more or less in accord with the more recent data. Calculations of total plankton are also of the same order of magnitude. Clarke's coastal water average of about 0.5 cc per m^3 was obtained in water of 40 m to 200 m depth, so that the total population is estimated to range from 20 cc to 100 cc per m^2 of sea surface. His estimate that the volume of the Sargasso Sea zooplankton is one-sixteenth to one-seventh the volume of the coastal crop would suggest in the former region an absolute volume of perhaps 0.03 to 0.08 cc per m^3. These are averaged over a depth range of about 900 m, indicating a total population of about 27 cc to 72 cc per m^2.

Returning to the more recent observations, rather different results were obtained on examination of the distribution of zooplankton organic matter. Fig. 18 shows that the coastal water was richer than the Sargasso Sea by a factor of three or four to one, and the Gulf Stream and the mean of the slope water stations were intermediate. These differences in distribution result from marked regional variations in the percentage of organic matter in the organisms. In the sample of coastal water plankton, the difference on ignition was 16.2% of the wet weight. By contrast, the slope water samples, consisting chiefly of salps, averaged 0.7%. The nontunicate fraction of the slope water population had an organic content of 5.8%, and in the Gulf Stream and Sargasso Sea it was respectively 5.1% and 4.8%.

The value obtained in coastal water falls within the rather large range of published values for zooplankton organic content. For example, Nakai (1942) found a range of 11% to 24% in analyses of nine species of crustacea, while Bogorov (1934) and Marshall, Nicholls, and Orr (1934) reported that the dry weight of *Calanus finmarchicus* varied from 15% to 50% of the wet weight.

The figures obtained from the slope water, Gulf Stream, and Sargasso Sea collections all were so much lower that they warranted further investigation. Material from qualitative surface tows was used for

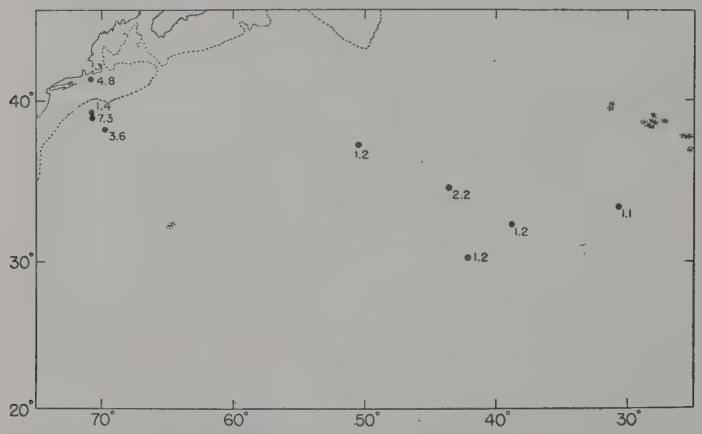

Figure 18. Zooplankton weight determinations. Estimated organic content of the total zooplankton population in grams per m² of sea surface.

analysis. First there was the question of the degree of compaction of the small Sargasso Sea samples and the amount of extraneous water that was entrapped with the animals in the so-called wet weight measurements. Four plankton suspensions of varying concentration were prepared in the usual way. Their wet weights were determined, and the general range was from 0.05 to 1.5 g. The samples were then blotted on filter paper and weighed again. The loss ranged from 20% to 30%. The organic matter averaged 7.1% of the second wet weight measurements, which still was considerably less than the published values.

Next, a few of the major constituents were measured separately. Salps, sagittae, euphausids, and large copepods were picked out individually. Nearly pure samples of pteropods were obtained by

decanting the rest of the catch. By pouring a plankton suspension through no. 2 silk and then through no. 10, a sample was caught on the no. 10 filter that consisted almost entirely of small copepods and juvenile crustacea. Again the excess water was removed by rolling the animals on filter paper, and the samples were then treated in the usual way, with the results shown in Table II.

TABLE II—Wet and Dry Weight, Organic Matter, and Ash of Representative Plankton Groups. Tunicates Collected in Slope Water, Others in Sargasso Sea

	Weight of sample in grams				*% of wet weight*		
	Wet	*Dry*	*Org. M.*	*Ash*	*Dry*	*Org. M.*	*Ash*
Tunicates	17.3678	0.2936	0.1092	0.1844	1.7	0.6	1.1
Pteropods	1.4496	0.5590	0.0969	0.4621	38.6	6.7	31.9
Euphausids	0.1403	0.0150	0.0130	0.0020	10.7	9.3	1.4
Sagittae	0.0469	0.0063	0.0046	0.0017	13.4	9.8	3.6
Copepods	0.1058	0.0184	0.0156	0.0028	17.3	14.7	2.6
Misc. small crustacea	0.4219	0.0404	0.0310	0.0094	9.5	7.3	2.2

Clearly it is not possible to ascribe the generally low organic content of the subtropical plankton to a preponderance of soft-bodied and watery animals such as salps and medusae. Of all the groups measured, only the large copepods had what has been considered to be a normal organic content. The reasons for this situation have not been investigated further, but the data by Nakai (1942) on the chemical composition of nine species of crustacea (seven copepods, one euphausid, one amphipod) suggest a simple solution. He found that the fat content of the crustacea was highly variable, ranging from 0.4% to 12.3% of the wet weight. The nonlipoid organic matter varied from 7.8% to 14.7% of the wet weight, and it will be noted that this is approximately the range of the total organic content of the Sargasso Sea crustacea. Nakai's collections were made in various locations in the Japan Sea between 32° and 42° N and 128° to 135° E. The southern, warm water animals generally had less fat than the northern ones. Thus the fat content of five samples taken between 32° and 35° N ranged from 0.4% to 3.0% of the wet weight, with a mean of 1.3%, while eight samples from 38° to 42° N ranged from 2.1% to 12.3%, with a mean of 6.9%. There was no overlapping of species in the regional groups, and hence no assurance that the observed differences were not simply peculiarities of the species in question. Nevertheless, there is a logical inference awaiting further proof that the scarcity of phytoplankton in the southern Japan Sea and the Sargasso Sea does not favor the accumulation of fatty reserves by the zooplankton and that this is responsible for the low content of organic matter.

ZOOPLANKTON RESPIRATION

A measurement was made of the oxygen consumption of coastal water zooplankton, using a part of the plankton sampler catch mentioned above. In the Sargasso Sea, eleven similar experiments were performed with material obtained from qualitative surface tows. The general method was to stir the plankton collection vigorously and remove for experimental purposes a sample of 10 to 30 ml, the size depending on the density of the catch. The sample was then put in a 350 ml oxygen bottle, and the bottle was filled with surface water and suspended in a tub of water on deck for twenty-four hours, after which the oxygen was measured and compared with the initial content of the surface water. In most cases there was also a control bottle of surface water exposed during the same period, permitting a correction for the respiration of organisms in the water added. The zooplankton not used for experimental purposes was preserved for later study.

In one respect, the coastal water and Sargasso Sea experiments were not strictly comparable. The former was done in the dark, the latter in clear glass bottles. According to the work on *Calanus finmarchicus* by Marshall, Nicholls, and Orr (1935), daylight approximately doubled respiration. However, this is not necessarily true of Sargasso Sea zooplankton. Several light and dark bottle experiments were performed with no. 20 net catches. They were originally intended as measurements of phytoplankton photosynthesis, but the quantity of net phytoplankton was so small that essentially they were experiments on zooplankton respiration. In this series the oxygen consumption in the light bottle averaged only 16% higher than in the dark.

TABLE III—Oxygen Consumption by Sargasso Sea Zooplankton

Date	*Oxygen*	*—ml per liter—*			*Mg C*	*—Zooplankton weight— (in mg)*		*—Carbon consumed—*	
	0 hrs.	*24 hrs.*	*Diff.*	*Control*	*consumed per day*	*Wet*	*Org. M.*	*% of Wet wt.*	*% of Org. M.*
30 VII	4.31	2.04	2.27	−.05	0.292	102	1.98	0.29	14.8
7 VIII	4.56	3.38	1.18	−.09	0.143	84	5.11	0.17	2.8
9 VIII	4.54	3.24	1.20	−.15	0.138	30	0.93	0.46	14.8
15 VIII	4.61	4.17	0.44	−.08	0.047	13	0.43	0.37	10.9
22 VIII	4.65	1.75	2.90	—	0.354	105	3.82	0.34	9.3
24 VIII	4.64	3.91	0.73	−.31	0.055	18	0.68	0.31	8.1
26 VIII	4.61	2.96	1.65	−.20	0.190	36	1.09	0.53	17.4
1 IX	4.21	2.24	1.97	−.10	0.245	25	1.43	0.97	17.1
2 IX	4.29	2.95	1.34	−.10	0.162	20	0.97	0.81	16.7
4 IX	4.17	2.48	1.69	—	0.210	87	5.27	0.24	4.0
10 IX	4.44	1.64	2.80	−.07	0.358	41	2.24	0.86	16.0

Details of the Sargasso Sea experiments are presented in Table III. They are listed only by date, but this is sufficient to identify the posi-

tion of the collection and correlated data by reference to the material in the APPENDIX. The first two columns show the initial concentration of oxygen in the experimental bottles and the concentration at the end of the twenty-four hour period. The difference, shown in the next column, is first corrected according to the control reading and then converted to an estimate of milligrams of carbon consumed per day by the zooplankton sample, assuming a respiratory quotient of unity. Zooplankton weights are listed as the quantities estimated to have been present in the experimental bottles. The actual quantities weighed were ten to fifty times these figures. Finally, the estimated respiratory requirements (carbon consumption) are calculated as percentages of the wet weight and organic content of the zooplankton.

The results are seen to vary widely. The average figures for daily carbon consumption are 0.49% of the wet weight and 12% of the organic matter. At the coastal station the carbon consumption was found to be 0.6% of the wet weight and 4% of the organic matter. Thus the respiratory rate per unit of zooplankton organic matter appears to be lower in the coastal water than in the Sargasso Sea, but with respect to wet weight the situation is reversed. The lack of agreement in the two kinds of measurements results from differences in the organic content of the two populations.

In view of the observed variability of the Sargasso Sea experiments, not much reliance can be placed on a single coastal water observation. However, the published data on *Calanus finmarchicus* provide an estimate of metabolic requirements that is probably more or less applicable to temperate water plankton in general. Marshall, Nicholls, and Orr (1935) estimated on the basis of oxygen consumption experiments that the food requirements of Calanus in summer were of the order of 2.5% to 7.6% of their organic content. Clarke and Bonnet (1939) obtained results that averaged considerably higher, although the range of variation of individual experiments overlapped considerably. In terms of daily carbon consumption, the values established by the two groups of investigators probably lie between 1.3% and 6.7% of the organic content of the animals. The single experiment on the mixed coastal water population falls approximately in the middle of this range, but the general level of the Sargasso Sea experiments is much higher. On the other hand, the food requirement per unit of wet weight (or volume) would appear to be more or less the same in both regions.

PHYTOPLANKTON-ZOOPLANKTON RELATIONSHIP

The data that have been presented on zooplankton organic content and metabolic requirements provide a means for instructive speculation on food problems. In the Sargasso Sea, with an average content of 2.2 mg of zooplankton organic matter per m^3, the average food requirement is estimated to be 0.26 mg of carbon per m^3 per day. This probably is equivalent to about 15 Harvey units, which amounts to a daily consumption of 8% of the surface phytoplankton population, and the total zooplankton population would require 20% of the total phytoplankton crop. In order to obtain the required amount of food, the daily filtration of a quantity of zooplankton containing 1 mg of organic matter (assuming 100% removal of phytoplankton) would be 2.2 liters. In the coastal zone, an average estimate of the zooplankton carbon requirement is 5.3 mg per m^3 per day, or 6% of the surface crop of phytoplankton. In order to meet its metabolic demands, a quantity of zooplankton equivalent to 1 mg of organic matter would need to filter only 70 ml of water per day, or about one thirtieth as much as the Sargasso Sea zooplankton. Thus either the latter feeds at a much faster rate, or, if the rates are more nearly equal, the coastal water zooplankton obtains far more food than is needed to satisfy its immediate demands.

This difference in what might be called the apparent minimum filtration coefficient may not actually be as large as it appears. In every respect the conditions of the Sargasso Sea investigation would be expected to lead to maximal results. The experiments lasted only a short time, and they were done in the light and at approximately surface water temperatures. At most they are applicable to immediate surface conditions, and the mean metabolic requirement for the whole population might be only a half or a third as much (7% to 10% of the phytoplankton population per day). Such a correction probably would bring the filtration coefficient down approximately to the level of the maximum feeding rates observed by Harvey (1937) in experiments with *Calanus finmarchicus*.

Supposing that gross activity, including feeding, varies more or less in accordance with the metabolic rate (Zeuthen, 1947, has presented some evidence favoring this view), there must be a great discrepancy in the food-gathering capacity of the two populations. Judging by the experiments on oxygen consumption and the ecological considerations presented above, the feeding rates may be about the same in the two areas, and at most they average three times as high in the Sargasso Sea. If the latter population was obtaining just enough food to permit survival, it seems likely that the coastal water zooplankton was con-

suming ten to thirty times as much food as it needed to satisfy its minimum requirements. Thus its apparent superiority in fatty reserves would be accounted for readily, but the differences in food gathering capacity are so large that it would also be necessary to postulate a vastly superior rate of herbivore reproduction in the coastal zone. According to the principles of dynamic balance, this would also imply a correspondingly higher rate of predation by the larger members of the food chain.

Admittedly there is some danger in attempting to arrive at broad conclusions without examining more of the seasonal cycle. A program of investigation is now underway which will provide more critical and comprehensive data on the plankton populations of the western North Atlantic.

SUMMARY

1. The material presented includes measurements of temperature and nutrient salts, analyses of phytoplankton pigments, wet weight and organic content of quantitative zooplankton collections, and experimental determinations of phytoplankton photosynthesis and zooplankton respiration. The observations were obtained at various positions in the western North Atlantic between New England and the Azores during the period of July to September, 1947.

2. The phytoplankton populations of the coastal and slope waters yielded pigment concentrations of 4,000 to 18,000 Harvey units per m^3, which is more or less normal for this season. In the Sargasso Sea the mean surface concentration was 140 units, and the total quantity averaged 49,000 units per m^2 of sea surface. Both figures are approximately one-sixth of the only previous measurements in this region, in May 1939.

3. Experimental measurements of the photosynthesis of surface water phytoplankton yielded values of 0.19 to 0.56 ml of oxygen per liter per day in the coastal zone and slope water. Oxygen changes in Sargasso Sea surface water were not significantly different from zero.

4. The observed vertical distribution of oxygen in the Sargasso Sea was such as to indicate that biological oxygen consumption exceeded production in the immediate surface layer and that production was dominant at a depth of around 50 m. By standard physical oceanographic methods it was estimated that there existed during the period of the investigation an average net oxygen production of 0.0012 ml per liter per day in the depth range between 25 m and 100 m. On the basis of these figures, a phytoplankton growth rate of 20% per day was postulated for the depth range specified, and the average growth rate for the whole population was estimated to be 6% per day.

5. Similar calculations based on the vertical gradients of nitrate and phosphate indicated what appeared to be relatively lower values for the utilization of these substances. It is pointed out that published data show a normal carbon-nitrogen-phosphorus ratio of 41 : 7.2 : 1 in plankton. The present calculations lead to an analogous estimate of the ratio of carbon production to nitrate utilization to phosphate utilization, but the closest approach to the published ratio that can be attained is 130 : 8.5 : 1. Certain ambiguities in the data are discussed. It remains undecided whether the results indicate actual nutrient deficiency or errors in the assumptions on which the calculation are based.

6. The average wet weight of zooplankton in the upper 400 m of water (or surface to near bottom in coastal water) was 0.84 g per m^3 in the coastal area, about the same in the slope water, 0.15 g in the Gulf Stream, and 0.045 g in the Sargasso Sea. In a deeper stratum of about 400 m to 800 m (uncorrected for wire angle) the quantity of zooplankton varied in different parts of the region from one-fifth to one-half the surface concentration. The averages for total zooplankton were of the order of 30 g wet weight per m^2 of sea surface in the coastal zone and Sargasso Sea, 70 g in the Gulf Stream, and upwards of 80 g in the slope water area.

7. The percentage of organic matter in the zooplankton catches varied widely from a maximum of 16.2 in the coastal collection to 0.7% in the slope water, the low value in the latter being due largely to the predominance of salps. The Sargasso Sea collections averaged 4.8% organic matter. Because of these differences, the regional distribution of zooplankton organic matter was quite different from that of wet weight, with a maximum of 4.8 g per m^2 of sea surface in the coastal water, 1.4 g in the Sargasso Sea, and intermediate values in the Gulf Stream and slope water. Indirect evidence suggests that these regional variations in organic content are largely due to differences in the quantity of stored lipoids (except for a few special cases such as the slope water salps), and this in turn is probably dependent on the concentration of phytoplankton.

8. Experiments on the metabolic rate of Sargasso Sea zooplankton yielded a wide range of results. The average, expressed in terms of daily carbon consumption, was 0.49% of the wet weight and 12% of the zooplankton organic content. A single experiment on coastal water zooplankton gave a value for carbon consumption of 0.6% of the wet weight and 4% of the organic matter per day, and these results are in good agreement with published data on the metabolic rate of *Calanus finmarchicus*.

9. A speculative discussion is presented of zooplankton food prob-

lems. It is estimated that in order to obtain its minimum food requirements, the Sargasso Sea zooplankton population would have to eat somewhere between 7% and 20% of the phytoplankton crop per day, and the coastal water zooplankton would have to eat 6% of the plant population. However, other considerations suggest that the actual consumption in the coastal zone is much greater. It is tentatively concluded that the zooplankton of the coastal zone is better fed than the Sargasso Sea population, which tends to account for its higher organic content and also suggests that it has a higher reproductive rate.

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APPENDIX

STATION* AND MISCELLANEOUS SURFACE ANALYSES. TEMPERATURE IN °C, PHOSPHATE AS MG-AT OF P PER M³, NITRATE AND NITRITE AS MG-AT N PER M³, PLANT PIGMENTS AS HARVEY UNITS PER M³

Station *Date* *N Lat.* *W Long.*	*Depth (meters)*	*Temp. (°C)*	*P*	*NO_3*	*NO_2*	*Plant pigments*
4603	1	23.8	—	1.7	.09	—
17 VII	100	14.0	—	6.3	.12	—
39–12	200	11.9	—	1.0	.02	—
70–29	300	9.1	—	—	.00	—
	400	7.1	—	6.5	.05	—
4604	1	26.2	—	.4	.00	—
20 VII	25	25.7	—	.7	.00	—
34–56	50	22.8	—	.6	—	—
65–34	100	22.1	—	1.3	.08	—
	150	19.1	—	2.2	.00	—
	200	18.8	—	2.2	.23	—
	300	18.4	—	2.4	.00	—
	400	17.8	—	4.1	.00	—
4605	1	27.7	—	.9	.06	—
25 VII	100	18.9	—	3.1	.02	—
33–30	200	18.9	—	2.3	.08	—
62–48	300	18.3	—	2.7	.05	—
	400	17.8	—	6.0	.15	—
4606	1	27.6	—	1.1	.07	—
26 VII	25	24.1	—	3.7	.07	—
35–04	50	21.3	—	.7	.10	—
60–36	100	19.2	—	2.3	.23	—
	150	18.8	—	2.5	.16	—
	200	18.4	—	4.6	.09	—
	300	18.1	—	2.6	.10	—
	400	17.5	—	5.2	.07	—
4607	1	26.3	.03	.0	.00	280
30 VII	100	20.3	.12	.0	.07	360
37–15	200	18.5	.10	1.9	.04	300
50–21	300	18.2	.11	2.3	.00	170
	400	17.8	.17	2.0	.00	ca .0
4608	1	25.0	.06	.8	.28	150
1 VIII	100	17.7	.10	2.6	.10	110
34–52	200	16.4	.31	4.7	.05	50
43–29	300	15.3	.37	3.7	.07	ca .0
	400	14.1	.47	6.4	.06	ca .0
4609	1	25.2	.07	.7	.17	70
3 VIII	100	17.8	.12	4.7	.15	ca .0
32–29	200	16.7	.21	3.2	.09	ca .0
41–00	300	15.6	.29	4.8	.08	ca .0
	400	15.1	.27	.7	.08	ca .0

* Tables include only the observations considered pertinent to the plankton problem. Precise temperature readings, oxygen concentrations and deep water distributions will be published subsequently.

Station Date N Lat. W Long.	*Depth (meters)*	*Temp. (°C)*	*P*	*NO_3*	*NO_2*	*Plant pigments*
4610	1	25.6	.00	.5	.15	—
7 VIII	25	25.4	.05	.2	.08	—
30–04	50	22.7	.02	.1	.10	—
42–02	100	19.8	.16	.0	.18	—
	150	18.7	.10	.7	.22	—
	200	17.8	.18	2.8	.18	—
	300	17.2	.25	4.2	.24	—
	400	16.0	.30	5.3	.12	—
4611	1	25.8	.10	.9	.10	190
13 VIII	100	17.7	.00	2.6	.08	210
32–22	200	15.9	.19	3.0	.08	160
38–50	300	14.9	.32	4.8	.07	—
	400	13.9	.44	7.0	.05	—
4612	1	25.4	.08	.0	.35	200
15 VIII	100	18.4	.01	1.0	.31	420
34–21	200	16.9	.23	3.8	.22	110
33–29	300	15.4	.31	4.7	.23	110
	400	14.5	.37	5.8	.31	—
4613	1	23.4	.04	.6	.29	—
21 VIII	25	22.8	.05	.3	.32	—
35–42	50	18.7	.01	.2	.21	—
27–47	100	16.0	.11	1.2	.39	—
	150	15.4	.21	4.0	.21	—
	200	14.7	.38	2.8	.26	—
	300	13.5	.51	7.3	.25	—
	400	12.5	.61	7.0	.11	—
4614	1	25.6	.06	.0	.20	—
23 VIII	100	19.2	.00	.7	.17	—
33–34	200	17.3	.17	4.1	.27	—
30–46	300	16.0	.25	6.5	.21	—
	400	15.0	.37	10.5	.20	—
4615	1	28.2	.05	.0	.18	—
31 VIII	25	27.0	.03	.0	.22	—
29–00	50	—	.03	.7	.16	—
48–31	100	21.8	.09	.8	.21	—
	150	—	.09	.0	.44	—
	200	18.4	.16	.9	.38	—
	300	—	.26	2.0	.22	—
	400	16.5	.35	5.7	.28	—
4616	1	29.0	.24?	.2	.25	—
2 IX	25	28.2	.00	1.0	.24	—
29–03	50	—	.04	.0	.28	—
55–18	100	20.6	.05	.0	.27	—
	150	—	.06	.9	.28	—
	200	18.3	.18	2.2	—	—
	300	—	.24	2.7	.22	—
	400	16.8	.28	3.1	.21	—

Station *Date* *N Lat.* *W Long.*	*Depth (meters)*	*Temp. (°C)*	*P*	*NO_3*	*NO_2*	*Plant pigments*
4617	1	29.2	.05	.0	.54	—
4 IX	25	28.8	.03	.7	.29	—
30–22	50	—	.00	1.1	.33	—
60–31	100	20.4	.00	1.3	.29	—
	150	—	.03	1.2	.35	—
	200	18.5	.04	1.7	.28	—
	300	—	.13	2.7	.24	—
	400	17.6	.20	4.0	.25	—
4618	1	28.5	.02	.0	.30	—
12 IX	25	28.5	.00	.0	.30	—
38–21	50	—	.00	1.0	.27	—
69–53	100	22.1	.01	.1	.26	—
	150	—	.03	.2	.29	—
	200	19.1	.05	.4	.33	—
	300	—	.15	1.9	.23	—
	400	17.7	.19	3.2	.20	—

Oxygen Concentrations (ml per l) Used to Compute Net Production

Station	*25 m*	*50 m*	*100 m*
4606	4.99	5.15	4.68
4610	4.62	5.36	5.05
4615	4.57	5.01	4.73
4616	4.69	5.35	5.10
4617	4.45	5.13	5.00

Surface Water Analyses

Date	*N. Lat.*	*W. Long.*	*Temp.*	*P*	*NO_3*	*NO_2*	*Plant pigments*
6 VIII	41–17	70–59	20.8	—	—	—	6,000
6 VIII	40–55	70–58	22.6	—	—	—	4,000
8 VIII	40–21	70–53	23.3	—	—	—	18,000
7 VIII	39–20	70–42	24.5	—	—	—	11,000
7 VIII	28–55	41–19	25.2	.12	.0	.14	190
9 VIII	32–00	42–26	25.6	.19	.0	.17	110
22 VIII	34–33	29–18	—	.03	.3	.00	110
24 VIII	33–07	32–29	25.6	.00	.0	.17	90
26 VIII	30–49	36–25	—	.08	.0	.23	100
30 VIII	29–00	44–44	—	.10	.0	.33	110
1 IX	29–03	51–34	28.2	.00	.0	.20	80
2 IX	29–02	54–50	—	.12	.0	.25	110
4 IX	30–19	60–07	29.0	.01	.0	.22	150
10 IX	34–17	65–55	29.2	.04	.0	.42	110

Contribution No. 442

THE EXCHANGE OF OXYGEN ACROSS THE SEA SURFACE[1]

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In temperate latitudes the oxygen content of sea water near the surface varies with the season. This results because the solubility of oxygen in the water changes with its temperature and because of the unequal production and utilization of oxygen by organisms at different seasons. Both factors cause an exchange of oxygen across the sea's surface. The present paper is an attempt to determine the magnitude of this exchange as it occurs in the Gulf of Maine and to evaluate the factors responsible.

The solution of the problem depends upon the assumption that the column of water underlying a square meter of sea surface and extending to a depth beyond which seasonal changes in chemical composition are insignificant may be treated as a closed system except for exchanges with the atmosphere. If Q_o represents the quantity of dissolved oxygen observed to be present in the column and ΔQ_o its change between two periods of observation, ΔQ_E the quantity entering through the sea surface, and ΔQ_x the net increase in oxygen resulting from biological activity during the time, then the equation representing the net exchange across the sea surface is

$$\Delta Q_E = \Delta Q_o - \Delta Q_x. \tag{1}$$

Negative values of ΔQ_o and ΔQ_x represent decreases in the dissolved oxygen in the column and negative values of ΔQ_E represent oxygen escaping to the atmosphere.

EVALUATION OF ΔQ_o AND ΔQ_x

The oxygen content of the column, Q_o, may be obtained by integrating the area enclosed by a curve representing the station data for

[1] Contribution No. 442 from the Woods Hole Oceanographic Institution.

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oxygen concentration and depth. From the difference in Q_o obtained at successive surveys ΔQ_o is estimated.

The net change in oxygen content due to biological activity, ΔQ_x, may be deduced from observed changes in inorganic phosphate content of the column, PO_4. In the process of photosynthesis a quantity of oxygen is set free proportional to the phosphate withdrawn from the water. Conversely, the oxidation of organic matter in metabolism sets free a quantity of phosphate corresponding to the oxygen consumed (Redfield, 1934; Fleming, 1941; Edmondson and Edmondson, 1947). In order to convert changes in phosphate into the quantities of oxygen set free or absorbed in the accompanying biological processes, use is made of an equivalence based on the observation (made in the waters of the Sargasso Sea) that the disappearance of 1 cc O_2 accompanies the appearance of 0.373×10^{-3} mg-at of phosphate phosphorus (Redfield, 1942)[2]. Correspondingly, the disappearance of 1 mg PO_4 is accompanied by the appearance of 28.3 cc O_2, or

$$\Delta Q_x = 28.3 \quad PO_4 .$$

Some uncertainty exists regarding the exactness of this relation in its present application, since it depends upon the assumption that in decomposition the process has gone to completion. Actually significant quantities of phosphorus are present in sea water at certain seasons in the form of dissolved organic compounds (Redfield, Smith and Ketchum, 1937). These do not contribute to the measurement of phosphate concentration; yet it cannot be doubted that their liberation was attended by some oxidation of associated organic matter. Increases in inorganic phosphate may consequently lag behind the attendant consumption of oxygen at the times and places where decomposition is occurring. Moreover, the value of the relation depends upon the average elementary composition of the organisms responsible, which may differ somewhat with time and place. Finally, the methods for determination of inorganic phosphate are not wholly satisfactory. Estimations of ΔQ_x are consequently subject to much greater errors than those of ΔQ_o.

DATA

The data examined were collected in the course of a survey of the Gulf of Maine made by the Atlantis in 1933–34. Eleven cruises were completed in the course of 15 months.

The area chosen for examination was the western basin of the Gulf,

[2] This equivalence is based on phosphate data uncorrected for salt error. See Cooper (1938).

a region of 200 to 250 m in depth lying between Cash's Ledge and the Massachusetts Coast. Within an area 35 miles square, lying between the latitudes 42° 15′ and 42° 50′ N and the longitudes 69° 10′ and 69° 45′ W, there were available from two to four sets of station data for each cruise[3].

The data were collected as part of a general hydrographic survey, and consequently no special provision was made to secure measurements designed to meet the special requirements of the present study.

In evaluating the quantity of oxygen and phosphate in the column under a square meter of surface at each period of observation, the data from the several stations occupied in the area were averaged. Oxygen data were available from three stations for each cruise except for January and August, when two stations were occupied, and for December, when four stations were occupied in the area. Phosphate data were available from three stations in September 1933, from two in July and December 1933 and in March and May 1934, and from one in January, April, June and September 1934. No data were available for October 1933 and August 1934.

It was assumed that seasonal changes in the quantity of oxygen in the water column are limited to a depth of 200 m and of phosphate to a depth of 100 m. Oxygen and phosphate contents were consequently integrated to these depths in estimating ΔQ_o and ΔQ_x.

The content of dissolved oxygen and of inorganic phosphate were both maximal in March. Consequently, it proved convenient to express ΔQ_o and ΔQ_x as the changes which have occurred or which will occur relative to the conditions obtaining at that time.

ASSUMPTIONS

The basic assumptions underlying the application of equation (1) are that exchanges of oxygen across the sides and lower surface of the water column have a negligible effect on its oxygen content and that equation (2) is valid. The latter assumption is sufficiently discussed above and in the references.

The assumption that exchanges resulting from the movement of oxygen or phosphate through the side walls of the column are negligible can be justified only by the consideration that the area of observation

[3] For data see Bulletin Hydrographique 1933 and 1934 M/Y Atlantis Stations Nos. 1699, 1703, 1721, 1747, 1748, 1749, 1856, 1857, 1858, 1864, 1865, 1875, 1876, 1909, 1910, 2022, 2023, 2024, 2074, 2075, 2076, 2168, 2169, 2170, 2220, 2221, 2236, 2258, 2259, 2273, 2274, 2275. Hydrographic observations were made by standard procedures. Oxygen was determined by Winkler's method and phosphate by the Denigès-Atkins procedure. The values for phosphate are not corrected for salt error.

is centered in a much larger region in which the horizontal distribution of components is uniform at any depth. The components which leave the column from one side by lateral mixing or flow may be supposed to be replaced almost exactly by those which enter from the opposite side. The seasonal changes in the concentration are so large compared to the gradients which are present in a horizontal direction at any time

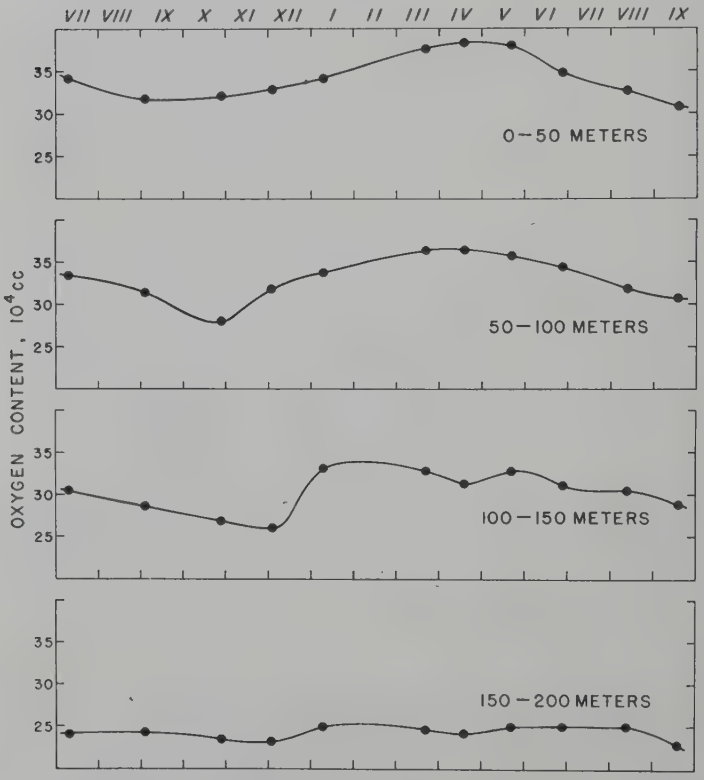

FIGURE 1. Seasonal variation of oxygen content of successive zones of 50 m depth beneath one m² of sea surface in Gulf of Maine.

that it seems unlikely that lateral transport has an important effect on the changes in the composition of the column.

The assumption that exchanges through the lower surface of the column are negligible requires

(1) that its depth be greater than that at which seasonal effects on the components can be observed and
(2) that the net movement of water from below by vertical mixing is insignificant.

The western basin of the Gulf of Maine is not sufficiently deep to permit the choice of a depth greater than 200 m for consideration. An examination of the samples collected periodically at greater depths shows only small fluctuation in oxygen content, and these do not appear to be related to the seasonal fluctuations observed at lesser depths. As a further check, the oxygen content of each 50-m length of the column has been estimated separately and the results plotted in Fig. 1. In the zone between 150 and 200 m the annual change in oxygen content is very small and amounts to only 10% of that of the entire 200-m column. Evidently failure to take account of seasonal changes which may occur at greater depths does not introduce significant errors.

A similar treatment of the phosphate data is shown in Fig. 2. The curve for the zone extending from the surface to 50 m shows a large seasonal fluctuation, which accounts for about 60% of the total seasonal change. The zone between 50 and 100 m also shows an increase in phosphate during the winter period. In the zones between 100 and 200 m there are fluctuations less clearly related to the general seasonal cycle and produced chiefly by low values obtained in January and April. Since there is no reason to think that phosphate concentrations would change in the deeper waters in this way, it is suspected that these fluctuations are due to systematic errors in the phosphate determinations during the cruises of January and April, such as might be occasioned by faulty standards. In order to avoid the multiplication of such errors, it has been assumed in the following consideration that the seasonal changes in phosphate below 100 m are negligible and that the best estimate of the changes in oxygen content due to biological activity are to be obtained from the phosphate content of the upper 100 m. Neglect of the changes in phosphate in the zone between 100 and 200 m reduces the estimated maximal seasonal variation of the column by only 20% and does not alter materially the general conclusions reached by this study.

Vertical mixing probably causes some exchange of oxygen and phosphate across the lower boundary. The deeper water of the Gulf has its origin through an inflow of slope water at the Eastern Channel, and

this water becomes fresher and colder as the western basin is approached, effects which can only be attributed to admixture with the overlying layers (Bigelow, 1927). It seems likely that there is a net upward movement of water as the result of this vertical exchange, in which an excess of deep water rises to escape from the Gulf in the surface currents across Georges Bank. The magnitude of this exchange cannot be evaluated and the phenomena require further study.

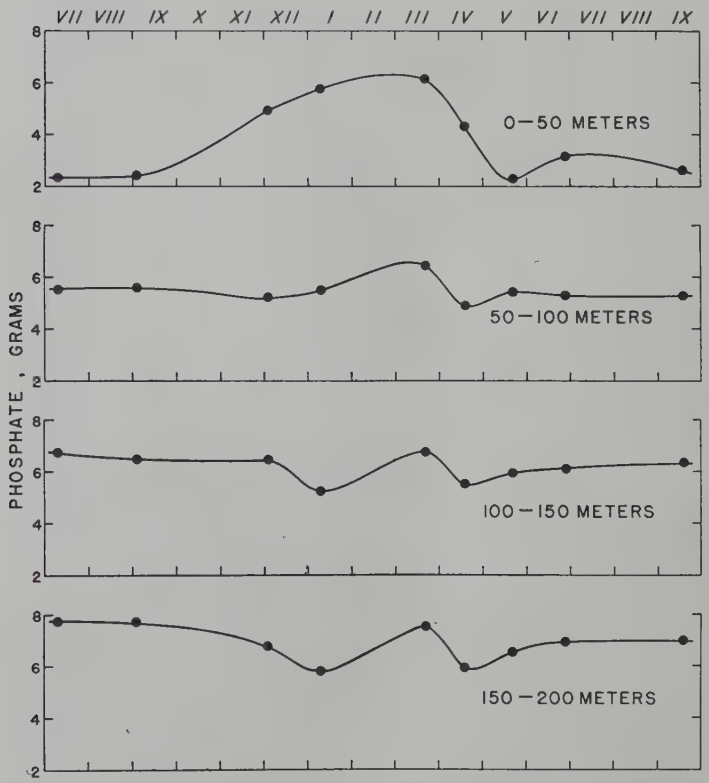

FIGURE 2. Seasonal variation of inorganic phosphate content of successive zones of 50 m depth beneath one m² of sea surface in Gulf of Maine.

It is likely, however, that such exchanges are small compared to the seasonal effects under consideration.

RESULTS

Table I records the results of the computations. The values obtained for ΔQ_o, ΔQ_x, and ΔQ_E are shown plotted against time in Fig. 3.

TABLE I. Oxygen and Phosphate Content of Water beneath One Square Meter of the Surface of the Gulf of Maine and the Seasonal Changes Estimated to Occur Relative to the Conditions Obtaining in March

Period of Observation	*1* Q_o 10^4 cc	*2* ΔQ_o 10^4 cc	*3* PO_4 g	*4* ΔPO_4 g	*5* ΔQ_x 10^4 cc	*6* ΔQ_E 10^4 cc
July 6–10, '33	122.2	−9.3	7.79	−4.86	13.7	−23.0
Sept. 4, '33	115.9	−15.6	8.17	−4.48	12.6	−28.2
Oct. 28–29, '33	110.4	−21.1	———	———	(10.0)	(−31.1)
Dec. 2–4, '33	113.8	−17.7	10.17	−2.48	7.0	−24.7
Jan. 9, '34	126.1	−5.4	11.27	−1.38	3.9	−9.3
March 22, '34	131.5	0	12.65	0	0	0
April 18, '34	130.1	−1.4	9.18	−3.47	9.8	−11.2
May 22, '34	131.3	−0.2	7.77	−4.88	13.8	−14.0
June 26–July 1	125.1	−6.4	8.44	−4.21	11.9	−18.3
August 11, '34	119.9	−11.6	———	———	(12.5)	(−24.1)
Sept. 19, '34	113.0	−18.5	7.89	−4.76	13.4	−31.9

Column *1* Q_o, oxygen content of column 1 m² × 200 m deep.
2 ΔQ_o, change in Q_o relative to March.
3 PO_4, inorganic phosphate content of column 1 m² × 100 m deep.
4 ΔPO_4, change in PO_4 relative to March.
5 ΔQ_x, change in oxygen content, corresponding to ΔPO_4, attributed to biological activity. It is assumed that ΔPO_4 and ΔQ_x are negligible below 100 m.
6 ΔQ_E, exchange of oxygen across 1 m² sea surface, relative to March.
Values in parentheses obtained by interpolation from curves in Fig. 3.

The annual change in the oxygen content of the water (maximum numerical value of ΔQ_o) is about 20×10^4 cc per m² of sea surface. The content is maximal in the latter part of March and minimal at the end of October.

The net annual change in oxygen content attributable to biological processes (maximum value of ΔQ_x) is about 13×10^4 cc per m² of sea surface. Oxygen production exceeds consumption during April and May. The processes are nearly balanced from June to September. Consumption exceeds production between October and March.

The annual exchange of oxygen across the sea surface (maximum numerical value of ΔQ_E) is about 30×10^4 cc per m². This quantity leaves the sea water during spring and summer and re-enters during the winter seasons. The turning points occur in the latter parts of October and March. The quantity of oxygen involved in the exchange is equal to that in a layer of air 1.5 m in depth.

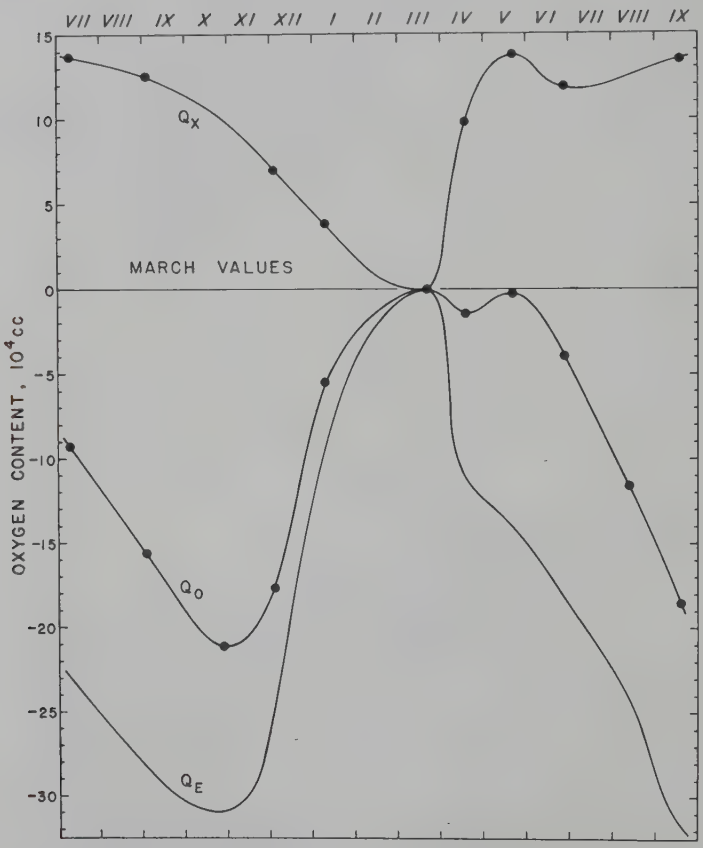

FIGURE 3. Seasonal values of ΔQ_o, the observed change in oxygen content, and ΔQ_x, the estimated change in oxygen content due to biological activity in the water beneath one m² of sea surface in Gulf of Maine, relative to the content observed in March. The curve ΔQ_E represents the quantities of oxygen estimated to have crossed one m² of sea surface between March and the time of observation. Negative values indicate losses of oxygen from the water.

Of the annual exchange across the sea surface only two-fifths may be attributed to the net production or consumption of oxygen by

organisms. The remainder presumably results from the effects of temperature changes on the solubility of oxygen in sea water.

Metabolic processes and solubility effects due to temperature supplement one another in producing the surface exchange. However, their relative importance differs with the season. In April and May practically all surface exchange is accountable by oxygen produced in photosynthesis. From June through September the metabolic processes are balanced and the continued surface exchange of oxygen accompanies the warming of the water. During the winter both processes contribute to maintaining the exchange; two-fifths of the oxygen absorbed from the atmosphere is consumed by organic activity and three-fifths held in solution by the cooling water.

THE OXYGEN PRESSURE HEAD ACROSS THE SEA SURFACE

Oxygen may be presumed to move across the sea surface as a result of the difference between the partial pressure of oxygen in the atmosphere and the tension, or escaping tendency, of the dissolved oxygen in the surface water.

If it is assumed that the air in contact with the sea surface is at the temperature of the water and is saturated with water vapor, the oxygen pressure of the atmosphere, P, will be $0.21\ (1 - w)$ atmospheres where w is the tension of aqueous vapor. The oxygen tension of the water, p, is equal to the oxygen pressure of the atmosphere when the water is in equilibrium with the atmosphere or is "saturated." Under other conditions it follows from Henry's law that $p = P\ C_x/C_o$, where C_o is the oxygen content of sea water in equilibrium with one atmosphere of moist air and C_x is the oxygen content of the sample in question. The head of oxygen pressure across the sea surface is consequently given by

$$P - p = P(C_o - C_x)/C_o, \tag{3}$$

when C_x is the oxygen content of water in the sea surface.

In order to evaluate $P - p$, data from the samples of water collected at a depth of one meter during each cruise have been averaged and the results are entered in Table II. In the direct estimation of P for application to the right-hand member of equation (3), allowance for the tension of water vapor in the atmosphere is inconsequential, since it reduces the value of P by only one or two per cent. In the estimation of $C_o - C_x$, however, it is important to take account of the water vapor in determining the value of C_o. Its value is proportional to P and will be reduced correspondingly as the vapor tension increases,

TABLE II. Estimates of $P - p$, the Pressure Head of Oxygen across Surface, and Averaged Data for Water at 1 Meter Depth on Which Estimate Is Based

Period of Observation	*Temp.* °C	*Salinity* °/oo	*P* atm	C_o cc/l	C_x cc/l	$P - p$ atm
July 6–10, '33	15.18	31.96	0.206	5.83	6.12	−0.010
Sept. 4, '33	19.55	31.56	0.205	5.38	5.72	−0.013
Oct. 28–29, '33	11.02	32.18	0.207	6.32	6.26	0.002
Dec. 2–4, '33	7.11	32.86	0.208	6.84	6.65	0.006
Jan. 9, '34	5.24	32.96	0.208	7.14	6.69	0.103
March 22, '34	2.92	33.07	0.208	7.54	7.47	0.002
April 18, '34	4.72	32.75	0.208	7.24	7.65	−0.012
May 22, '34	9.19	31.65	0.208	6.59	7.27	−0.021
June 26–July 1, '34	14.95	31.93	0.207	5.89	6.28	−0.014
August 11, '34	18.45	31.96	0.205	5.49	5.89	−0.015
Sept. 19, '34	17.65	32.12	0.206	5.56	5.88	−0.012

the reduction amounting to as much as 2% at the warmer seasons. Since the difference between C_o and C_x does not exceed 10% and at most seasons is 6% or less, neglect of the correction for vapor tension will lead to substantial error in estimating $C_o - C_x$.

To determine C_o, values in the table of Fox (1909) for the quantity of oxygen dissolved in sea water in equilibrium with *dry* air have been corrected to take account of the reduction in partial pressure of oxygen in an atmosphere saturated with water vapor. An alignment chart constructed from these values has been used to estimate C_o from the observed temperature and salinity of the water samples for which C_x was measured.

The estimate of the values $P - p$ for the period of survey is plotted in Fig. 4. During the winter the pressure is positive, favoring a movement of oxygen from the atmosphere into the water. During the summer the pressure is reversed. The maximum positive value of 0.013 atmospheres was found in January, while the maximum negative value of 0.021 atmospheres occurred in May. The changes in direction come in October and March. These relations are consistent with the movements of oxygen across the sea surface deduced from measurements of oxygen and phosphate in the water column beneath the surface.

THE COEFFICIENT OF OXYGEN EXCHANGE

The rate of exchange of oxygen across the sea surface is defined theoretically by the equation

$$dQ/dt = E \cdot S \cdot (P - p), \tag{4}$$

where dQ/dt is the rate at which exygen enters the surface, S is the surface area and E is a constant, the exchange coefficient. E may conveniently be given the dimensions cc O_2/month $\times$ m^2 $\times$ atmosphere.

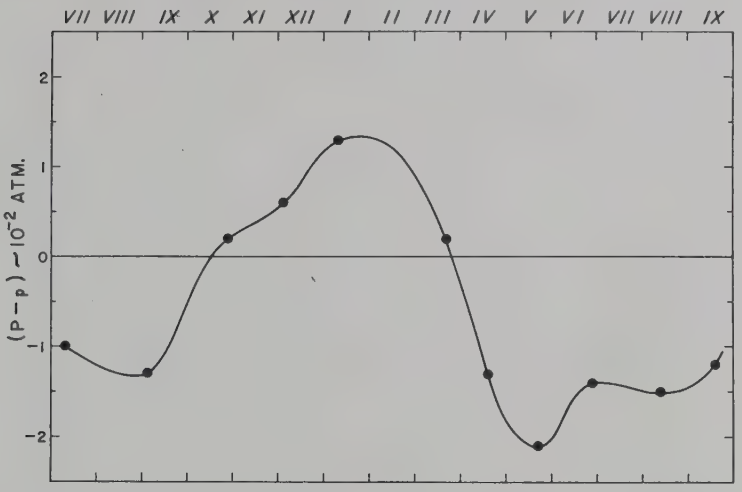

FIGURE 4. Seasonal variation in the pressure head of oxygen, $P - p$, across the surface of the Gulf of Maine. Negative values represent a pressure of oxygen in the water greater than in the atmosphere, a condition favoring the escape of oxygen from the sea water to the atmosphere.

Values of E may be estimated from equation (4), taking dQ/dt to equal the amount of oxygen entering the surface between successive times of observation divided by the time in months between the observations, and by expressing $P - p$ by the average of its values at the beginning and end of the intervening period. These approximations will not lead to large errors for periods when ΔQ_E and $P - p$ are relatively constant or are changing at nearly constant rates. The estimations are not reliable when the curve describing these functions are undergoing inflection, since at such times the average values may differ greatly from the properly weighted mean. Estimates of the value of E obtained in this way are given in Table III.

The three estimates made between the end of October and the latter part of March when $P - p$ is positive, indicating a movement of oxygen into the sea water, yield an average value for E of 11.3×10^6. The value for January 9–March 22 is suspect, because the average value of $P - p$ is unreliable, being obtained when the curve is undergoing inflection. The two values obtained between October 29 and January 9 are in close agreement and give the most reliable estimate

TABLE III. ESTIMATES OF THE COEFFICIENT FOR THE EXCHANGE OF OXYGEN ACROSS THE SURFACE OF THE GULF OF MAINE

	1	*2*	*3*	*4*	*5*
Period of Observation	Δt	ΔQ	$\Delta Q/\Delta t$	$(P - p)_m$	E
July 8–Sept. 4	1.8	−5.2	−2.9	−0.0155	2.5
Sept. 4–Oct. 29	1.8	−2.9	−1.6	−0.0055	2.9
Oct. 29–Dec. 3	1.2	6.4	5.3	0.0040	13.2
Dec. 3–Jan. 9	1.2	15.4	12.8	0.0095	13.5
Jan. 9–Mar. 22	2.4	9.3	3.9	0.0075	5.2
Mar. 22–Apr. 18	0.9	−11.2	−12.4	−0.0050	24.8
Apr. 18–May 22	1.1	−3.8	−3.5	−0.0165	2.1
May 22–June 28	1.1	−4.3	−3.9	−0.0175	2.2
June 28–Aug. 11	1.5	−5.9	−3.9	−0.0145	2.7
Aug. 11–Sept. 19	1.3	−7.8	−6.0	−0.0135	4.4

Column *1* Δt is interval between observations—in months.

2 ΔQ is quantity of oxygen entering surface during interval, *i. e.*, the change in ΔQ_E values of Table II. Unit: 10^4 cc/m².

3 $\Delta Q/\Delta t$ is mean rate of exchange during interval. Unit: 10^4 cc/m² × months.

4 $(P - p)_m$ is mean of values of oxygen pressure head $P - p$ at beginning and end of interval. Unit: atmospheres.

5 E is exchange coefficient of oxygen. Unit: 10^4 cc/month × m² × atmosphere.

for E for the period when oxygen is entering the sea surface as 13×10^6.

Of the estimates made during the remainder of the year, when $P - p$ is negative, that for March 22–April 18 is unusually large. Its reliability may be questioned, because at that time the estimate of the oxygen exchange is based almost wholly on changes in the phosphate concentration of the upper layers of water. The resulting value for E is entirely subject to the errors in this estimation. The six remaining estimates are in fair agreement and yield an average value for E of 2.8×10^6. The exchange coefficient for the period when oxygen is leaving the sea may be fixed approximately at this value.

These estimations indicate that the exchange coefficient of oxygen at the sea surface is greater during the winter period when oxygen is being taken up by the water than during the summer period when the movement of oxygen is in the opposite direction. The values for E for these two periods appear to be approximately 13×10^6 and 2.8×10^6 respectively.

DISCUSSION OF THE COEFFICIENT OF OXYGEN EXCHANGE

The only pertinent data on the rate of movement of oxygen across an air-water interface of which I am aware are those of Bohr, Krogh, and Adeney and Becker. In studying the absorption of oxygen by small bubbles at 37° C, Krogh (1910) obtained a value of 0.0776 cc per minute per cm² per atmosphere, which, when converted to the dimensions in which E has been expressed, equals 33.5 x 10^6 cc per month

per m^2 per atmosphere. Adeney and Becker (1920) measured the quantity of oxygen leaving a relatively large bubble in its passage through unsaturated water. Estimates by Dorsey (1940: 552–555) based on their data give values of about 0.017 cc per minute per cm^2 per atmosphere or, when converted into the presently employed units, 7.3×10^6 cc per month per m^2 per atmosphere. Adeney and Becker's results indicate that the coefficient is about 5% lower for sea water and that it is not materially changed by temperature.

The present estimates for the sea surface agree in magnitude with these measurements. The values of Adeney and Becker are actually spanned by the estimates made for the summer and winter periods.

The difference in the value of the exchange coefficient between summer and winter is sufficiently distinct to suggest that some real differences in the conditions near the sea surface at these seasons affect the exchange. Before accepting this conclusion it is desirable to examine the assumption that the air immediately over the sea surface is saturated with water vapor. The introduction of the correction for water vapor causes the values of $P - p$ to be smaller in winter and larger in summer than would be the case if the atmosphere were assumed to be dry or incompletely saturated. The values of E are consequently made larger in winter and smaller in summer. Thus the application of this correction might produce seasonal differences in the estimated value of E of the sort observed.

To determine whether the assumed saturation of the atmosphere could produce the seasonal difference obtained for E its values for the periods December 2–January 9 and June 26–August 11 have been calculated, assuming the atmosphere over the sea surface to be dry. The results give values of 10.5×10^6 for the former period and 3.7×10^6 for the latter. The results obtained, assuming a saturated atmosphere, were 13.5×10^6 and 2.7×10^6 respectively. It is evident that the difference in the winter and summer values of E cannot be attributed in any major degree to possible error in this assumption.

The possibility that the difference in the value of E depends directly on the seasonal difference in temperature is ruled out by Adeney and Becker's measurements on bubbles.

Two conditions suggest themselves in explanation of the seasonal difference in E. The values are calculated on the assumption of a flat sea surface of unit area. Waves, spindrift, and the bubbles entrained by white caps, which all tend to increase the air-water interface within a given area, are much more prominent in winter, favoring higher values of E at that time. Also, conditions near the sea surface in summer are much more stable than in winter. There is greater probability that the air immediately over the surface is saturated with

water vapor and that small scale gradients of oxygen concentration exist immediately beneath the sea surface. The use of oxygen analyses from samples collected at a depth of one meter in estimating the pressure of oxygen in the surface water leaves much to be desired. In winter, when unstable conditions favor boisterous mixing, this procedure is probably adequate, but in summer it is likely that the water at the sea surface is more nearly in equilibrium with the atmospheric oxygen than the sample collected. This appears to be the most important consideration in accounting for the seasonal difference in the estimated values of the coefficient of oxygen exchange. Taken together the several factors considered are sufficient to account for the results.

SUMMARY

1. It is estimated that about 30×10^4 cc of oxygen per m^2 leaves the surface of the Gulf of Maine between the end of October and the latter part of March, a like amount re-entering from the atmosphere during the alternating period.

2. The net production and consumption of oxygen by organisms is sufficient to account for two-fifths of this exchange, the remainder being attributable to the effects of temperature on the solubility of oxygen.

3. In April and May the production of oxygen in photosynthesis is sufficient to account for the entire surface exchange; during the summer the exchange is attributable chiefly to decreasing solubility resulting from the warming of the water. In late fall and winter, excess oxygen consumption and increasing solubility are both responsible for the exchange.

4. The pressure head of oxygen across the sea surface has been determined and found to agree in direction with the estimated movement of oxygen.

5. The exchange coefficient of oxygen is estimated to be about 13×10^6 cc per m^2 per atmosphere per month in winter. In summer a value of 2.8×10^6 is obtained.

6. The seasonal difference in the values obtained is attributed to conditions at the sea surface, such as sea state and stability, which cause errors in the measurements and estimations.

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Contribution No. 443

Reprinted from JOURNAL OF METEOROLOGY, Vol. 5, No. 5, October, 1948, pp. 243–246
Printed in U. S. A.

INHOMOGENEITIES OF TURBULENCE, TEMPERATURE, AND MOISTURE IN THE WEST INDIES TRADE-WIND REGION

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(Manuscript received 21 January 1948)

1. Introduction.—During the period 10–28 April 1946, an expedition was made to San Juan, Puerto Rico, to investigate convection cells in the atmosphere.[3] On most days of observation, two- to four-tenths of cumulus was observed, occurring in patches, so that clear areas with a diameter greater than 100,000 ft existed between them. This paper will be concerned with the characteristics of these clear areas.

Soundings taken in the clear areas show a dry-adiabatic lapse rate in the lowest 2000 ft, in which the mixing ratio hovers about a constant value. Near 2000 ft, a slight inversion or isothermal layer exists, and above it a temperature lapse rate of about 2.2C per 1000 ft is maintained, which is conditionally stable, since the saturated-adiabatic lapse rate is about 1.4C per 1000 ft in the relevant temperature range. The trade inversion is found at heights varying between 6000 and 9000 ft, with an average near 7500 ft. Between inversions, the mixing ratio decreases by about 1.1 g kg^{-1} per 1000 ft. Since the inversion at 2000 ft corresponds to the base of the clouds, and the inversion at 7500 ft represents the upper limit of all but the largest clouds, this height interval is called the "cloud layer," in spite of the fact that the regions under discussion are cloudless.

Owing to the long over-water trajectory and the relatively isothermal sea surface, advective and diurnal changes of temperature and mixing ratio may be disregarded. Nevertheless, horizontal traverses made at heights between 150 and 7500 ft do not show homogeneity of temperature or moisture. The purpose of this paper is to describe the fluctuations and to discuss their origin.

2. Instrumentation of aircraft.—A PBY-5A (Navy patrol plane) was fitted with a psychrograph, accelerometer, and angle-of-attack recorder. The accelerometer, which was constructed by the Woods Hole Oceanographic Institution,[4] records the vertical

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[3] The field work was carried out under contract with the Bureau of Ships, and study of the results is being continued under contract with the Office of Naval Research.

[4] A. C. Vine, "Accelerometer for air turbulence measurements in aircraft," memorandum on file at the Woods Hole Oceanographic Institution, August 1945.

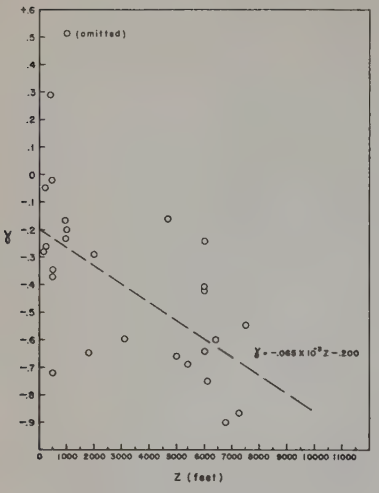

FIG. 1. Height variation of correlation between temperature and mixing ratio.

accelerations of the plane on an Esterline Angus recorder. Since the displacements are small and irregular, this record is approximated by a series of instantaneous readings. Each gust is assumed sinusoidal, and the area is integrated in such a way that the absolute value of the velocity, rather than the net effect, is obtained. When the necessary conversion factors are entered, the velocity, v', becomes

$$v' = \tfrac{1}{8}NP \text{ m sec}^{-1},$$

where N is the number of divisions (=0.02 ma) from crest to trough, and P is the period in seconds, or fractions thereof.

The angle-of-attack recorder was developed by Specialties, Inc.[5] It records the change in the angle at which the wind strikes the plane. The tangent of this angle, or, approximately, the angle in radians, represents the ratio between the vertical velocity not measured by the accelerometer, v'', and the air speed. This relationship is used in the form

$$v'' = 0.36\ N \text{ m sec}^{-1},$$

where N is the number of divisions (=0.02 ma) from crest to trough.

The sum, $v' + v''$, was assumed to be the vertical velocity, v. The letter v is used instead of the usual w, in order to prevent confusion with the mixing ratio, which will be discussed below.

The mixing ratio was calculated from the dry-bulb and wet-bulb temperatures, T_d and T_w, respectively, which had been measured by the psychrograph [2]. It was assumed that the traverses were made at constant pressure. The mixing ratio corresponding to the wet-bulb temperature, w_{iw}, was read from a pseudo-adiabatic diagram, and the mixing ratio, w, was calculated from the psychrometer equation in the form

$$w \times 10^3 = w_{iw} \times 10^3 - 0.4(T_d - T_w).$$

Since T_d and T_w may be assumed to be correct to ± 0.1C [2], the probable errors in computing w would be materially those of w_{iw}, which may be assumed to be ± 0.1 g kg^{-1}.

3. Results of observations.—The dry-bulb and wet-bulb temperature traces were evaluated independently. Points of inflection in the autographic records were sufficiently close to being equally spaced that it was assumed that no artificial weighting would be introduced by using these temperatures in statistical analysis.

The standard deviation of the temperature, σ_T, expressed in tenths of degrees C, increases from an average of 1.07 below 1000 ft to an average of 3.81 near 6000 ft. Simultaneously, the standard deviation of the mixing ratio, σ_w, expressed in tenths of a gram per kilogram, increases from 2.71 to 9.66. These values are given in detail in table 1. Since deviations of this order correspond to vertical displacements of about 900 ft (at the 6000-ft level), they were well beyond any possible error due to variations from horizontal flight, which were of the order of ± 50 ft.

TABLE 1. Summary of data.

Date (April)	Height (ft)	v (m sec^{-1})	γ	σ_T (0.1C)	σ_w (0.1 g kg^{-1})	σ_{T^w} (0.1C)
10	170	0.71	−0.28	0.7	1.6	0.4
	1800	0.55	−0.65	0.9	4.0	0.6
	3100	(0.48)†0.37	−0.60	5.3	7.0	—
	5400	0.13	−0.69	1.2	3.2	0.9
	7500	—	−0.54	13.3	19.2	11.7
12	500	—	−0.34	1.0	1.9	0.9
	6800	—	−0.90	3.0	7.2	1.8
13	950	—	−0.16	1.6	3.1	1.5
	7250	—	−0.86	5.4	11.3	3.6
17	200	0.74	−0.05	0.6	2.8	0.7
	950	0.73	−0.23	1.2	2.6	1.2
	2000	0.40	−0.29	2.0	2.4	1.7
	5000	0.14	−0.66	4.8	11.3	3.8
22	1000	0.77	−0.20	0.9	2.9	0.8
	6000	0.15	−0.64	4.4	14.6	3.2
23	500	0.74	−0.72	0.8	2.9	0.5
	1000	0.48	+0.52	6.5	4.1	—
	5900	0.23	—	—	—	—
	6100	0.25	—	—	—	—
	6270	(0.61)†0.26	—	—	—	—
25	6375	0.10	−0.60	1.5	8.6	1.3
26	440	0.67	−0.02	1.4	3.2	1.6
	4650	0.17	−0.16	2.4	1.8	2.2
	6000	0.11	−0.24	1.2	5.4	1.2
27	220	0.71	−0.26	0.8	1.8	0.4
	400	0.70	+0.29	1.6	4.3	—
	6000	0.16	−0.41	4.9	11.3	—
	6100	0.14	−0.75	2.2	20.1	2.8
28	500	0.55	−0.37	2.4	3.2	—
	6000	0.25	−0.42	1.5	2.0	—

† Includes cloud turbulence.

[5] Specialties, Inc., "Angle of attack recorder on a PBY-5 airplane," Specialties Report R175, Serial No. 2.

In order to measure the effect of a change in temperature on the mixing ratio, the correlation between mixing ratio and temperature was calculated for each run. With the exception of two correlations—both in the homogeneous layer, and one through a rain shower —they were all negative. There was considerable scatter, but the general trend was toward an improvement of the correlation with height (fig. 1). Omitting the traverse through rain, the equation for this relationship, obtained by least squares, is

$$\gamma = -0.065 \times 10^{-3}z - 0.200,$$

where γ is the correlation coefficient and z is the height in feet.

The scatter of these points prohibits too great reliance on the equation above, but the figure does show that at the lower heights, where the temperature fluctuations are small, the fluctuation of the mixing ratio is more or less haphazard, while at the greater heights, where the temperature deviations are comparatively large, a commensurate inverse variation of the mixing ratio might be expected. This suggests that the virtual temperature is more constant than the dry-bulb temperature. Calculation of σ_{T^*}, the standard deviation of the virtual temperature, for all traverses through clear air, shows that it is in general smaller than σ_T^*, and to a greater extent in the larger deviations.

The relative constancy of the virtual temperature permits some estimate of the amount by which the mixing ratio will vary for any given temperature change. However, it does not explain the initial cause of the fluctuations. The obvious explanation was in terms of turbulence, so the records of the accelerometer and angle-of-attack meter were first examined. The average absolute value of the vertical component of the wind was evaluated for each traverse, and plotted against height (fig. 2). On April 17, the air-speed indicator and altimeter were inoperative, so that the values obtained on that date must be considered as doubtful, and are marked as such. They are included because of the paucity of data for the heights traversed.

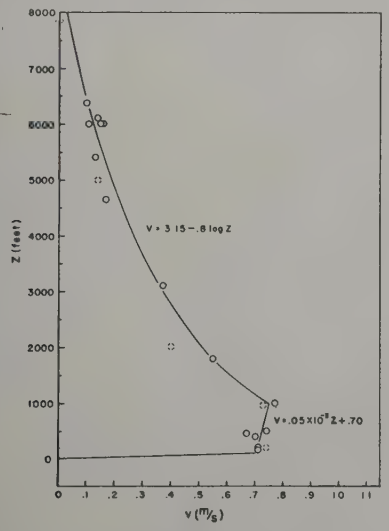

Fig. 2. Height variation of average turbulence, in the clear.

Within the region from 150 to 1000 ft, the average vertical velocity was nearly constant, and its increase with height was found, by the method of least squares, to be

$$v = 0.05 \times 10^{-3}z + 0.70,$$

where v is the velocity in m sec^{-1} and z is the height in feet.

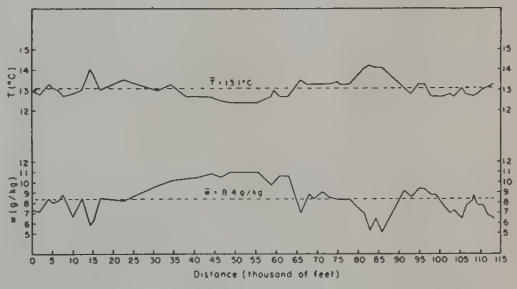

Fig. 3. Sample horizontal traverse, 22 April 1946, at 6000 ft.

Within the cloud layer, all cloud turbulence was omitted from the averages. A value of 0.75 m sec^{-1} at 1000 ft was found from the above equation. At 7500 ft, a value of 0.05 m sec^{-1} was indicated by the data. A logarithmic decrease with height was assumed between these two values, and was found to fit the points well. The equation is

$$v = 3.15 - 0.8 \log_{10} z,$$

where the units are the same as before.

The temperature fluctuations, however, cannot be explained by these turbulence records. Inspection of the temperature traces on the traverses made near 6000 ft shows that there is frequently a distance of about 30,000 ft between the crest and trough of the record (fig. 3). Since the turbulence records show an average diameter of 100 ft at this level, this scale of turbulence could not be the primary cause of the temperature fluctuations.

4. Possible causes of the temperature fluctuations.— Since the fluctuations are not dependent on the small-scale turbulence, an explanation was sought in the larger-scale phenomena. The photogrammetric map of

the sky, made by this project,[6] indicates that a cloud diameter of 30,000 ft is a good estimate of the smaller clouds which existed near the extremely wide clear areas. This suggests two possible explanations, not necessarily mutually exclusive.

Since the cloud heights were continually changing, it is entirely possible that a region which was clear at the time of observation, had a partial cloud cover only a few hours previously. As a cloud dissipated, it would leave a residue of air cooler and more moist than its surroundings. The turbulence records show that gusts of cloud dimensions dissipate rapidly after the cloud ceases to be visible, so that whatever temperature and moisture variations exist after a cloud dies down would not be rapidly wiped out by vertical transfer. Lateral mixing would then have the greater effect in the process. Pilot-balloon observations taken at San Juan show that the wind shear is very slight in the cloud layer, and the nearly vertical development of the clouds suggests that this condition exists over the water north of San Juan. As a result, lateral mixing would be extremely slow. Under these conditions, the assumption that the virtual temperature would be the quantity to be most nearly homogeneous along the horizontal for several hours after the cloud dissipated does not seem to be unreasonable.

The variations in the size of the standard deviations at any given height would then be due to differences in the strength of the cloud turbulence before it had dissipated, since on that would depend the temperature and moisture variations remaining in the air after the cloud abated.

Another theory which fits the available data is that of convection cells. These cells would extend from the inversion at 2000 ft to that at 7500 ft, and would be half the period of the temperature trace, or 30,000 ft in diameter. The diameter of the type of turbulence which would cause such cells is much larger than could be measured on the instruments described above. The largest horizontal temperature and moisture fluctuations would be expected at 2000 and at 7500 ft. When the small-scale turbulence profile given above is superimposed on this circulation, it seems to have the effect of wiping out any signs of the cells at 2000 ft. With the exception of the run at 2000 ft, taken on April 17, no inversion of turbulence is shown at the base of the cells. The fact that the inversion of temperature appears as markedly in clear areas as it does near clouds might be accepted as evidence in favor of the cell theory. In order for these cells to exist in a steady state, a continuous source of energy would be necessary. This source could be cool moist air at the top of the cell, a warm dry upsurge at the base, or some combination of the two.

As an approximation of the temperature difference necessary for this circulation, the 'parcel' equation [1] yields 2.2C. This value is obtained by assuming that the parcel will move at the dry-adiabatic lapse rate, so that no entrainment would take place. However, frictional forces have been omitted, so that a more realistic picture would require a slightly larger value.

When the usual amplitude of 1.0C at 6000 ft is extrapolated upward to 7500 ft, at the lapse rates indicated, a 2.2C difference from the surrounding air is obtained. Moreover, on the traverse at 7500 ft, made on April 10, a virtual temperature range of 5.4C was observed. However, on this occasion two small clouds were encountered during the flight, so that the temperature range is probably larger than would be encountered in clear air. Nevertheless, these data indicate that the order of magnitude necessary to initiate this type of circulation at the top of the cell is very near the observed values. Since the only apparent source of this moisture is the residue of dissipated clouds, this can only be considered as a maintained temperature difference in a limited sense. Due to small-scale mixing, the temperature trace showed no fluctuation of the required magnitude near the base of the cells. It is possible that a small positive increment occurs at this level. This would have the effect of reinforcing circulation set up from the upper limit of the cell.

5. Conclusions.—Since the temperature fluctuations are largest in the nonturbulent air, and the temperature and moisture vary oppositely, making the virtual temperature more constant than the dry-bulb temperature, the assumption that these fluctuations are initially caused by dissipated clouds seems probable. A definite decision as to whether the circulatory movement of convection cells is then set up must await further investigation of this region, with special emphasis on the turbulence, temperature, and moisture characteristics of the boundaries of such cells. Unless it can be proved that the necessary temperature difference can be maintained, the convection-cell type of circulation could exist in only a limited sense of the steady state.

[6] J. Wyman, and collaborators, "Vertical motion and exchange of heat and water between the air and the sea in the region of the trades," Woods Hole Oceanographic Institution, 1946 (unpublished).

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Contribution No. 445

THE EFFECT OF OCEAN CURRENTS ON INTERNAL WAVES

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In a fluid whose density changes with the height, either abruptly at a sharp surface of discontinuity or gradually, it is possible to have internal wave motions whose amplitude is greatest at the density discontinuity or, in the case of a gradual density change, somewhere in the interior of the fluid and not at the free upper surface where the surface waves have their maximum amplitude. The occurrence of such internal waves has been demonstrated by Ekman (1904), Seiwell (1937, 1942), Ufford (1947), and others. A review of our theoretical and empirical knowledge of internal waves has been given by Sverdrup, *et al.* (1942: 585–602). In the theoretical investigations it has always been assumed that the mean velocity of each layer, *i. e.*, the velocity apart from the wave motion, is zero. In many cases, especially where ocean currents are present, this assumption will not be satisfied. It is the purpose of the present paper to investigate whether or not modifications in the internal wave motion would be brought about by the existence of such currents on which the internal wave motion may be superimposed.

The presence of undisturbed currents on which the wave motions are superimposed complicates considerably the expressions for the wave periods, wave velocities, amplitude ratios at different levels, etc. Therefore, a very simple model will be considered which consists of two fluid layers (Fig. 1). The free upper surface (0) may be at the level $z = 0$, the rigid lower surface (2) at the level $z = -H$. Both fluids are separated by an internal boundary at the level $z = -h^I$. Each of the two fluids is incompressible and homogeneous, the densities being ρ^I and ρ^{II}, respectively, for the upper and lower fluid layers. The velocities in both layers, in the absence of wave motion, are U^I and U^{II}, respectively, both parallel to the x-axis. These current

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velocities may also be assumed to be constant within each layer and to change abruptly at the surface of discontinuity. In the absence of wave motion the pressure distribution is given by the expression

$$P = g\rho z + \text{const.},$$

where ρ is the density and g the acceleration of gravity. The wave motion may be considered as a small perturbation superimposed on the horizontal current U, and the velocity components in this case may be $U + u$, w while the pressure is $P + p$. Under the assumption that the perturbation quantities are small (designated by small letters), the equations of motion and continuity may be written

$$\begin{aligned} &\frac{\partial u}{\partial t} + U\frac{\partial u}{\partial x} + \frac{1}{\rho}\frac{\partial p}{\partial x} = 0\,, \\ &\frac{\partial w}{\partial t} + U\frac{\partial w}{\partial x} + \frac{1}{\rho}\frac{\partial p}{\partial z} = 0\,, \\ &\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} = 0\,. \end{aligned} \tag{1}$$

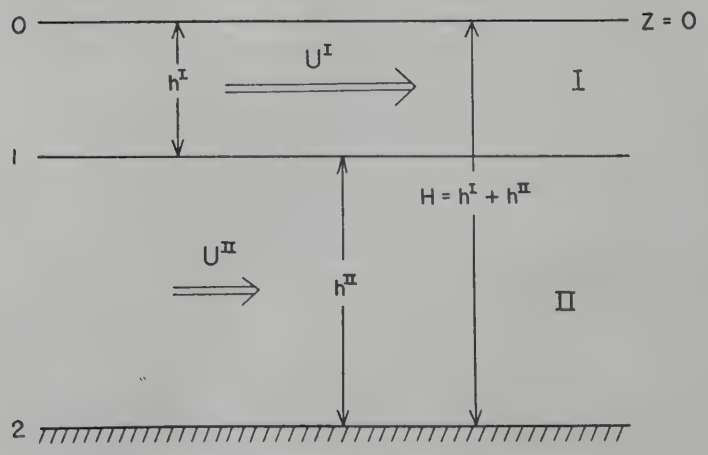

Figure 1. Stratification of fluid.

The equation of continuity is satisfied if a stream function ψ exists, such that

$$u = -\frac{\partial \psi}{\partial z}, \quad w = \frac{\partial \psi}{\partial x}. \tag{2}$$

Since the rigid lower boundary at $z = -H$ must be a stream line, the solution of (1) for the lower layer in the case of waves travelling in the x-direction may be written in the form

$$\psi^{II} = K^{II} \sinh \alpha(z + H)\, e^{i(\alpha x - \beta t)}, \tag{3}$$

$$p^{II} = -\alpha c^{II} \rho^{II} K^{II} \cosh \alpha(z + H)\, e^{i(\alpha x - \beta t)}. \tag{4}$$

Here, K^{II} is an arbitrary constant, $\alpha = 2\pi/L$, where L is the wave length, $\beta = 2\pi/T$, where T is the period, $c = \beta/\alpha$, the wave velocity, and $c^{II} = c - U^{II}$.

For the upper layer, the solution of (1) may be written in the form

$$\psi^{I} = (K_1{}^{I} e^{\alpha z} + K_2{}^{I} e^{-\alpha z})\, e^{i(\alpha x - \beta t)}, \tag{5}$$

$$p^{I} = -\alpha c^{I} \rho^{I} (-K_1{}^{I} e^{\alpha z} + K_2{}^{I} e^{-\alpha z})\, e^{i(\alpha x - \beta t)}, \tag{6}$$

where $K_1{}^{I}$ and $K_2{}^{I}$ are arbitrary constants and where $c^{I} = c - U^{I}$. Since at the free surface the pressure must remain constant,

$$P^{I} + p_{z=0}{}^{I} = -g\rho^{I} z + \alpha c^{I} \rho^{I} (-K_1{}^{I} + K_2{}^{I})\, e^{i(\alpha x - \beta t)} = \text{const.} \tag{7}$$

In the expression for p^{I} the actual height of the free surface has been replaced by the height of the free surface in the undisturbed position, $z = 0$. This simplification involves only an error of higher order. It follows that the equation of the free surface may be written in the form

$$z - Z_0\, e^{i(\alpha x - \beta t)} = \text{const.}, \tag{8}$$

where the amplitude of the free surface

$$Z_0 = \frac{\alpha}{g} c^{I} (-K_1{}^{I} + K_2{}^{I}).$$

The kinematic boundary condition requires that a particle which was once part of the free surface remains in this surface. If in general the equation of the disturbed free surface is

$$F + f = 0,$$

where $F = 0$ denotes the equation for the undisturbed boundary, the kinematic condition becomes

$$\left(\frac{\partial}{\partial t} + U^{I} \frac{\partial}{\partial x}\right) f + w_{z=0}{}^{I} \frac{\partial F}{\partial z} = 0.$$

Here, only an error of higher order is involved if the value of w at the actual disturbed position of the boundary is replaced by the value at the undisturbed position. The last equation leads to the following equation for Z_0,

$$c^I Z_0 = -(K_1{}^I + K_2{}^I) .$$

By means of the two expressions for Z_0, (5) and (6) may be written as follows:

$$\psi^I = -Z_0\left[\frac{g}{\alpha c^I}\sinh \alpha z + c^I \cosh \alpha z\right] e^{i(\alpha x - \beta t)} \tag{9}$$

$$p^I = \alpha c^I \rho^I Z_0\left[\frac{g}{\alpha c^I}\cosh \alpha z + c^I \sinh \alpha z\right] e^{i(\alpha x - \beta t)} . \tag{10}$$

The equation of the internal boundary, which, in the absence of wave motion, is $z = -h^I$, is given by the condition that the pressure at this discontinuity must be continuous. There are two kinematic boundary conditions which express the fact that particles in the upper as well as in the lower layer, which at one time were at the boundary, must remain there. Similar to the procedure in the case of the free surface, these conditions permit one to express the arbitrary constant K^{II} in (3) and (4) by the amplitude of the internal boundary Z_1,

$$K^{II} = -\frac{Z_1 c^{\cdot\cdot}}{\sinh \alpha h^{II}} . \tag{11}$$

Furthermore, the ratio of the amplitudes of the free surface Z_0, and of the internal boundary Z_1, is found to be

$$\frac{Z_1}{Z_0} = -\frac{g}{\alpha c^I{}_2}\sinh \alpha h^I + \cosh \alpha h^I , \tag{12}$$

and the wave velocity c must satisfy the equation

$$c^{I4} + \sigma a^I a^{II} c^{I2} c^{II2} - \frac{g}{\alpha}\sigma(a^{II} c^{II2} + a^I c^{I2}) + \frac{g^2}{\alpha^2}(\sigma - 1) = 0. \tag{13}$$

Here the following abbreviations have been used:

$$\frac{\rho^{II}}{\rho^I} = \sigma, \quad \coth \alpha h^I = a^I, \quad \coth \alpha h^{II} = a^{II} .$$

The amplitudes Z_0 and Z_1 of the free and of the internal boundary give the amplitudes of the vertical motion at the levels $z = 0$ and $z = -h^I$ where the two boundaries are situated in the undisturbed case. In order to find the amplitude z of the vertical motion at other

levels, an additional integration has to be performed. If again quantities of higher than the first order in the perturbation terms are neglected,

$$\frac{dz}{dt} = \frac{\partial z}{\partial t} + U\frac{\partial z}{\partial x} = w .$$

By integration of this equation, for the upper layer it follows that

$$z^I = \left(\frac{g}{\alpha c^{I^2}} \sinh \alpha z + \cosh \alpha z\right) Z_0 \, e^{i(\alpha x - \beta t)} ,$$

and for the lower layer, if the expression (11) is used for K^{II},

$$z^{II} = \frac{\sinh \alpha \, (z + H)}{\sinh \alpha h^{II}} Z_1 \, e^{i(\alpha x - \beta t)} . \tag{14}$$

At the internal boundary, $z = -h^I$, the vertical displacements in both layers must be the same, which leads again to the relation (12). If by means of this relation Z_0 in the foregoing expression for z^I is replaced by Z_1,

$$z^I = \frac{(g/\alpha c^{I^2}) \sinh \alpha z + \cosh \alpha z}{-(g/\alpha c^{I^2}) \sinh \alpha h^I + \cosh \alpha h^I} Z_1 \, e^{i(\alpha x - \beta t)} . \tag{15}$$

As (14) shows, the amplitude of the vertical motion increases from zero at the bottom, $z = -H$, to Z_1 at the internal boundary, $z = -h^I$. In the upper layer the amplitude of the vertical motion at a given depth depends on the magnitude of c^I in addition to the parameters which determine the vertical amplitude in the lower layer. It is necessary, therefore, first to determine the wave velocity c from (13).

A rigorous solution is quite complicated because equation (13) is of the fourth degree, but approximate solutions can be obtained without much difficulty. For this purpose the conditions in the absence of currents, $U^I = U^{II} = 0$, may first be reviewed briefly. Let $\varepsilon = (\rho^{II} - \rho^I)/\rho^I$, which in all actual cases is small compared to unity. If powers higher than the first of ε are neglected, the following two well known roots of (13) are obtained:

$$c_1^2 = \frac{g}{\alpha} \frac{a^I + a^{II}}{1 + a^I a^{II}} \left[1 + \varepsilon \frac{a^{I^2} + a^{II^2} - a^{I^2} a^{II^2} - 1}{(a^I + a^{II})^2 (1 + a^I a^{II})}\right] \tag{16}$$

(surface wave)

and

$$c_2^2 = \frac{g}{\alpha} \frac{\varepsilon}{a^I + a^{II}} . \tag{17}$$

(internal wave).

The bracket in (16) is very closely equal to one and may be replaced by this value. The expressions for c_1^2 and c_2^2 show that, of the four roots of (13), the two for the internal waves are considerably smaller than the other two, at least as long as the density discontinuity is small, a condition which is always true for internal boundaries in the ocean.

For this reason it may now be assumed that in the more general case where U^I and U^{II} are not both zero, the values of c^I and c^{II} for the internal waves are also sufficiently small so that the first two terms in (13) may be neglected, these being of the fourth and third degree in these quantities. The solution of the remaining quadratic equation,

$$\sigma\,(a^{II}c^{I^2} + a^I c^{I^2}) - \frac{g}{\alpha}(\sigma - 1) = 0\,, \tag{18}$$

results in the following expression for c,

$$c = \frac{U^I a^I + U^{II} a^{II}}{a^I + a^{II}} \pm \left[\frac{g}{\alpha}\frac{\rho^{II} - \rho^I}{\rho^{II}}\frac{1}{a^{II} + a^I} - \frac{(U^I - U^{II})^2}{(a^I + a^{II})^2}\,a^I a^{II}\right]^{\frac{1}{2}}. \tag{19}$$

In order to obtain a correction to this approximation let the rigorous solution of (13) be $c + j$, where j is a small quantity if c is a good approximation. If $c + j$ is substituted for c in (13), if powers higher than the first in j are neglected, and if it is taken into account that the value of c given by (18) makes the combination of the last two terms in (13) equal to zero, the following expression is obtained for the correction j to the approximate wave velocity

$$\left[4c^{I^3} + 2\sigma a^I a^{II} c^I c^{II}(c^I + c^{II}) - 2\frac{g}{\alpha}\sigma\,(a^{II}c^{II} + a^I c^I)\right] j = -\,c^{I^4} - \sigma a^I a^{II} c^{I^2} c^{II^2}\,. \tag{20}$$

It should be noted that the value for c to be inserted in this formula is the one given by (19). For any particular numerical example it is simplest to check the approximation represented by (19) by direct computation of the correction term j from (20).

After the wave velocity c has been determined, the distribution of the vertical amplitude can be found from (14) and (15). As (14) shows, the velocity of the undisturbed current does not affect the distribution of the vertical amplitude in the lower layer if the amplitude of the internal discontinuity Z_1 is taken as the basic constant. But

U^I and U^{II} affect the value of the vertical amplitude in the upper layer, since (15) contains $c^I = c - U^I$, and since c depends on U^I and U^{II}. However, it can be seen that the effect of the current on the distribution of the vertical amplitude as a function of the depth will be small. With the actually occurring current velocities, c^I will be considerably smaller than g/α. Consequently, the first terms in the numerator and denominator of (15) will be considerably larger than the second terms, except very close to the free surface, $z = 0$. Consequently

$$z^I \approx -\frac{\sinh \alpha z}{\sinh \alpha h^I},$$

except in the closest vicinity of the free surface, and the distribution of the vertical amplitude is practically independent of the current velocity.

In order to amplify this statement, consider the smallest possible value of g/α for which the waves do not become exponentially unstable. In this case the square root in (19) is zero, so that

$$\frac{g}{\alpha} = \frac{(U^I - U^{II})^2}{a^I + a^{II}} a^I a^{II} \frac{\rho^{II}}{\rho^{II} - \rho^I},$$

and

$$\frac{g}{\alpha c^{I2}} = \frac{a^I + a^{II}}{a^{II}} a^I \frac{\rho^{II}}{\rho^{II} - \rho^I}.$$

Since the percentual density difference $(\rho^{II} - \rho^I)/\rho^{II}$ is a small quantity, $g/\alpha c^{I2}$ could be comparable to one only if $(a^I + a^{II})a^I/a^{II}$ were small. But since a^I is a hyperbolic cotangent it cannot be less than one, and it follows that a^{II} would have to be negative, which is impossible.

The case of long waves may also be considered separately. When the wave length is large compared to the depth of the fluid layer, the hyperbolic cotangent may be replaced by the reciprocal of its argument. The expression (19) for the velocity of the internal wave then becomes

$$(21) \quad c = \frac{U^I h^{II} + U^{II} h^I}{H} \pm \left[g \frac{h^I h^{II}}{H} \frac{\rho^{II} - \rho^I}{\rho^{II}} - \frac{(U^I - U^{II})^2 h^I h^{II}}{H^2} \right]^{\frac{1}{2}}.$$

Further, since the hyperbolic sine may be replaced by its argument, from (14)

$$z^{II} = \frac{z + H}{h^{II}} Z_1 \, e^{i(\alpha x - \beta t)} \,, \tag{22}$$

and since the hyperbolic cosine may be replaced by one,

$$z^{I} = \frac{\dfrac{gz}{c^{I^2}} + 1}{-\dfrac{gh^{I}}{c^{I^2}} + 1} Z_1 \, e^{i(\alpha x - \beta t)} \,. \tag{23}$$

Equation (21) shows that in the case of long waves the vertical amplitude increases linearly from the bottom to the internal boundary, as is well known in the absence of a basic current.

It can be shown similarly that in the upper layer the vertical amplitude decreases practically linearly from its maximum value at the internal boundary to the free surface. This statement is certainly true as long as the depth h^I of the upper layer is not very small, because for sufficiently large h^I the first terms in the numerator and denominator of (22) are much larger than one. Only for very small depths z the first term in the numerator of (22) will be of the order one, but at these levels the vertical motion due to the internal waves is very small anyway. If h^I is small compared to the total depth H of the fluid, it follows from (20) that approximately

$$c^{I^2} = gh^I \frac{\rho^{II} - \rho^I}{\rho^{II}} - \frac{(U^I - U^{II})^2 \, h^I}{H} \,.$$

If $h^I = 10$ m, $H = 1000$ m and $(\rho^{II} - \rho^I)/\rho^{II} = 2 \cdot 10^{-3}$, for instance,

$$\frac{gh^I}{c^{I^2}} \sim \frac{\rho^{II}}{\rho^{II} - \rho^I} \,,$$

so that the first terms in the denominator and numerator of (22) are still considerably larger than unity except very close to the surface, where the amplitude is very small, as pointed out before.

In order to show the modifications in the wave velocity produced by a current, the following example may be considered:

$$\rho^I = 1.024 \qquad \rho^{II} = 1.026$$
$$h^I = 100 \text{ m} \qquad h^{II} = 3000 \text{ m}$$
$$L = 1000 \text{ m}.$$

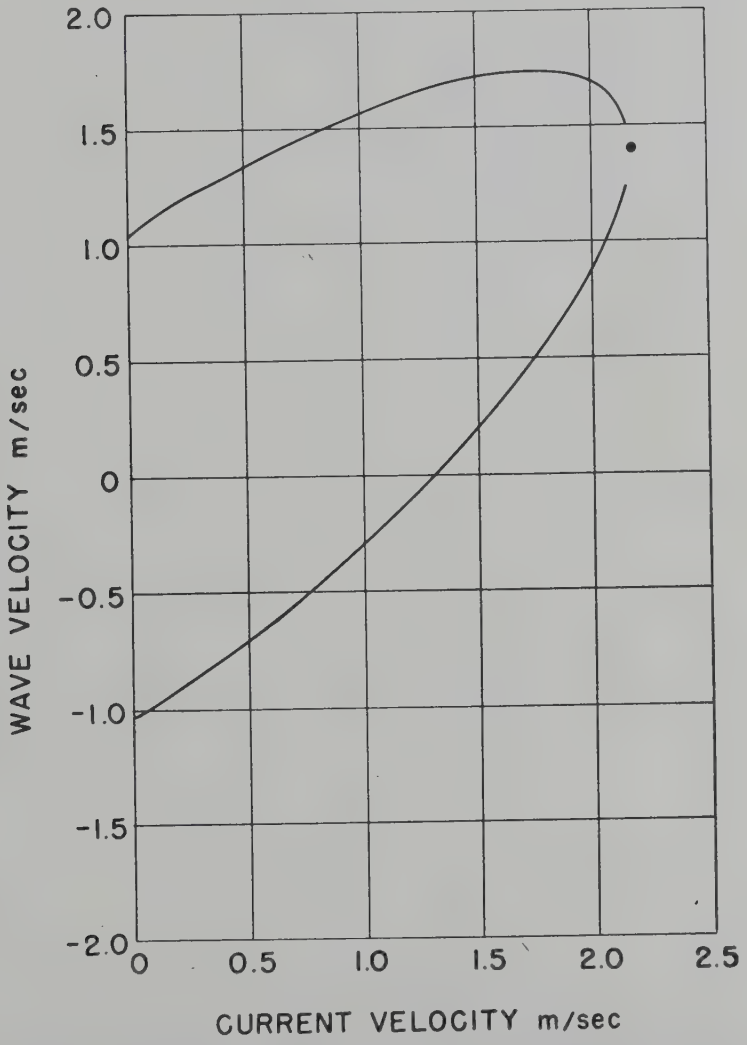

Figure 2. Wave velocity for different current velocities. (Density discontinuity 0.2%, depth of upper layer 100 m and of lower layer 3,000 m, wave length 1,000 m.)

The fluid in the lower layer may be at rest. In Fig. 2 the wave velocity is plotted as a function of the current velocity U^I in the upper layer. For each value of U^I two different values of c exist, depending on whether the positive or the negative sign before the square root is taken. The two solutions for c become identical when $U^I = 2.18$ m/sec, which represents the limit between stability and instability. The value of c for this value of U^I is indicated by a dot in Fig. 2, but the two curves are not joined here for the sake of clearness.

The depth distribution of the amplitude of the vertical motion can be computed from (14) and (15). The result is shown in Fig. 3 for the foregoing numerical example. As just explained, the velocity of the undisturbed current has only a very small effect on this distribution, and the curve shows consequently well known features, *viz.*, a rapid decrease from the internal boundary to the free surface in the relatively shallow surface layer and a less rapid decrease from the internal boundary to the bottom through the relatively deep lower layer.

As mentioned previously, only very close to the free surface does the amplitude of the vertical motion change substantially with different speeds of the undisturbed current. This fact is clearly shown by (12), which gives the amplitude ratio of the two boundaries. But even though the percentual variation of this ratio with different current velocities can be very large, its practical significance is very small, because the oscillation of the free surface produced by internal waves is negligible in any case.

Finally, the horizontal motion due to internal waves may be considered briefly. A certain modification of this motion occurs, of course, because it is now superimposed on basic currents, not on a state of rest. In addition, the amplitude of the horizontal motion will also be modified somewhat, as can be shown in the following manner. According to (9) and (12),

$$u^I = \alpha c^I Z_1 \frac{(g/\alpha c^{I^2}) \cosh \alpha z + \sinh \alpha z}{-(g/\alpha c^{I^2}) \sinh \alpha h^I + \cosh \alpha h^I} e^{i(\alpha x - \beta t)} \tag{24}$$

and according to (3) and (11),

$$u^{II} = \alpha c^{II} Z_1 \frac{\cosh \alpha (z + H)}{\sinh \alpha h^{II}} e^{i(\alpha x - \beta t)} . \tag{25}$$

In the numerator and denominator of (23) the second terms are, for most of the layer, much smaller than the first terms, as discussed before, so that u^I is largely proportional to c^I. Similarly, u^{II} is proportional to c^{II} according to (24). Any modifications in the value of

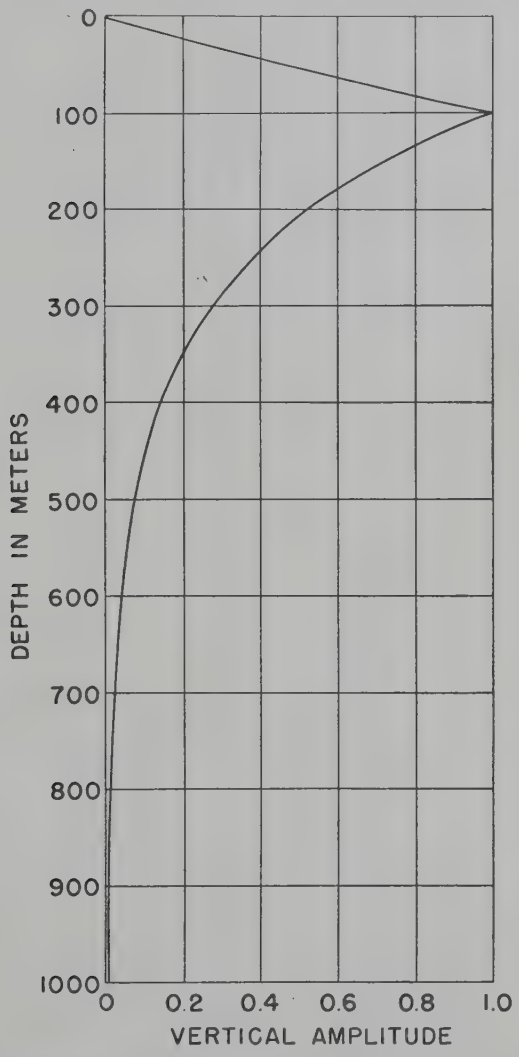

Figure 3. Distribution of the amplitude of the vertical motion as function of depth (amplitude at the internal discontinuity equal to one).

c caused by the existence of an undisturbed current will therefore be reflected in the amplitudes of u^I and u^{II}.

SUMMARY

The effect of a basic current on internal waves in the ocean is studied. It is shown that, while the wave velocity is modified by the existence of such a current, the distribution of the vertical amplitude of the wave motion as a function of the depth is very little affected by the presence of an ocean current. The amplitude of the horizontal motion is modified to a certain extent by the presence of ocean currents.

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Contribution No. 447

NEW GENERA AND SPECIES OF BATOID FISHES[1]

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INTRODUCTION

The trawling campaigns carried out by the research vessel ATLANTIS of the Woods Hole Oceanographic Institution along the north and south coasts of Cuba during the winter of 1938 and spring of 1939, under the joint auspices of the University of Havana and of Harvard University, brought to light along the 200–500 fathom zone an abundant population of small skates (Family Rajidae), the existence of which had not previously been suspected there. Their discovery emphasizes the desirability of a more thorough exploration of the benthonic fish-fauna, especially for elasmobranchs of this general depth zone in the West Indian region as a whole, as well as at greater depths along the North American slope. The necessity of assigning these Cuban skates—representing several new species—to their correct taxonomic positions calls for some discussion of generic definitions within the large troublesome family to which they belong.

Some of them, with one other skate that has long been known, form a homogeneous group that is characterized by the shortness of the rostral projection from the cranium; a new genus, *Breviraja*, is proposed for these.

Two others of the new Cuban skates are of more general interest, for they illustrate an extreme modification of the pelvic fins. These fins, among elasmobranch fishes as a whole, diverge but little from what may be regarded as their primitive state, for they retain the broad base, have but little power of independent motion, and their outer margins are only moderately deeply concave, if at all so. However, each of the pelvics of these two Cuban skates is subdivided into

[1] Drawings by E. N. Fischer.

[2] Contribution No. 447 from the Woods Hole Oceanographic Institution.

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two entirely separate lobes; the anterior lobe is slender, limb-like and arises independently from the lower surface of the disc, while the posterior one is much broader and fin-like, its anterior edge merging with the inner posterior margin of the corresponding pectoral fin. This modification of the pelvics is shared by two species of Rajidae from the Natal Coast of South Africa,[3] by the little-known genus *Anacanthobatis* Von Bonde and Swart (1924: 18, pl. 23) from Natal, and by one genus (*Typhlonarke*) of electric rays; otherwise it appears to be unique among batoids so far as known. Moreover, in these two Cuban species the modification of the pelvics is accompanied by a short extension rearward of each lateral bar of the pelvic arch itself beyond the point of articulations of the most posterior of the three or four radial cartilages borne by it; furthermore, the first two or three radials that are ordinarily borne along the anterior part of the basipterygial cartilage have been lost. The resultant gap (Fig. 1) corresponds to the external gap between the two subdivisions of the pelvic fin. Thus, the anterior pelvic division includes only the three or four radials that arise directly from the pelvis itself, whereas in all other skates, in which the condition in this regard is known, the anterior division includes these radials as well as the first two or three radials that are borne along the anterior part of the basipterygial cartilage. This specialization of the pelvic skeleton and fin is so remarkable that we have no hesitation in invoking it as the basis for a new genus, for which we propose the name *Cruriraja*, roughly translatable as "skates with legs."

A second major departure from the usual elasmobranch morphology is found in the conformation of the nostril of the little electric ray from the Pacific Coast of Central America, described as *Discopyge ommata* Jordan and Gilbert (1890). In all other electric rays, so far as known, the nostril is a simple aperture, more or less narrowed but not interrupted in its midsector. We have checked this feature in *Torpedo*, in *Narcine*, in *Hypnos*, in *Benthobatis* and in *Narke*. Such is the usual state of the nostril among the batoids as a whole, and no essential departure from this condition seems to have been reported previously for any elasmobranch. However, examination of a female and a male of *D. ommata*, loaned us by John Tee-Van of the New York Zoological Society, shows that each of the nostrils is divided into two separate apertures by a cross bridge about midway of its length. The outer of the two apertures constitutes the exposed and visible part of the nostril, whereas the inner aperture is entirely roofed over by the joint curtain-

[3] *Raja parcomaculata* and *R. durbanensis* Von Bonde and Swart (1924: 9, 11, pl. 21, fig. 2, pl. 22, fig. 1).

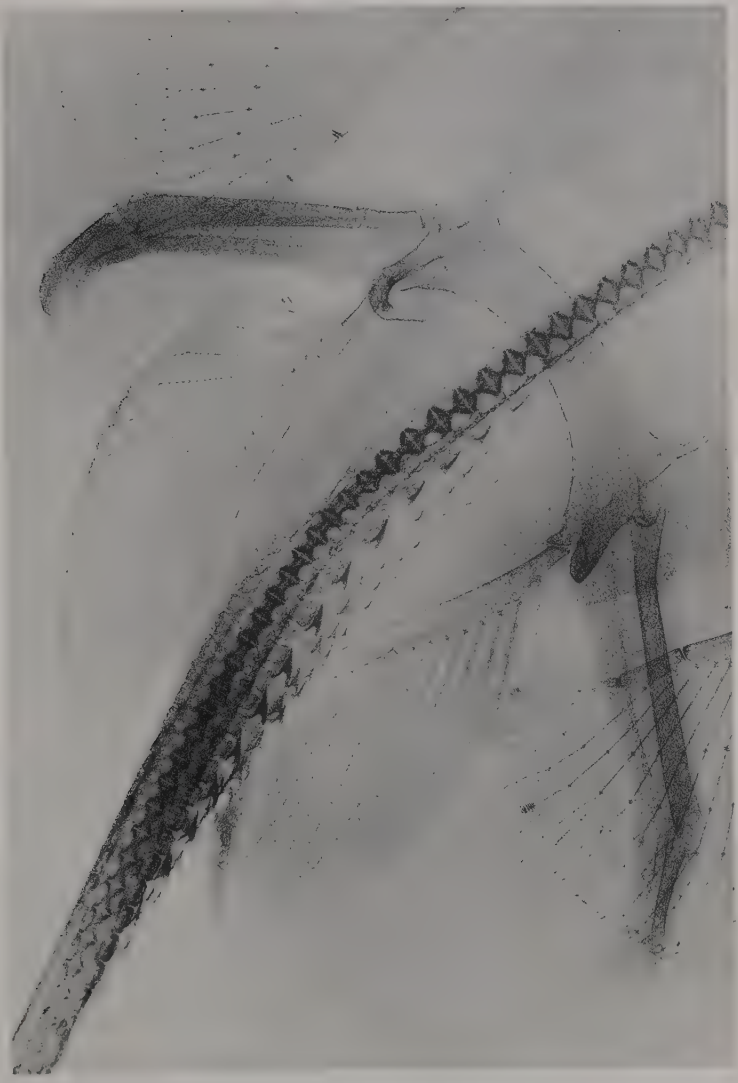

Figure 1. *Cruriraja poeyi*, sp. nov., female, type, 328 mm. long, Harv. Mus. Comp. Zool. No. 36324. X-ray photograph unretouched, showing the gap between radials borne on the pelvis and those on the anterior part of the basipterygial cartilage.

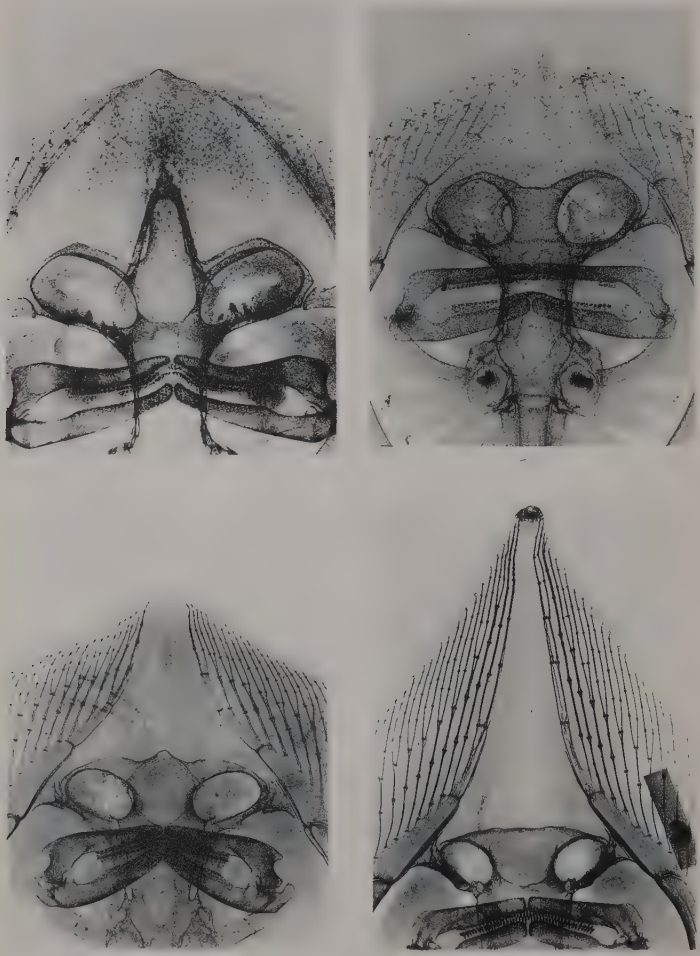

Figure 2. X-ray photographs, slightly retouched, showing front of cranium and rostral cartilage, where present, together with forward extension of pectoral rays. Upper left, *Breviraja colesi*, sp. nov. (Harv. Mus. Comp. Zool. No. 36374); upper right, *Psammobatis scobina* (Philippi, 1857), female, about 190 mm. long, from Uruguay (U. S. Nat. Mus. No. 86721); lower left, *Sympterygia microps* (Günther, 1880), female, about 475 mm. long, off Buenos Aires, Argentina (U. S. Nat. Mus. No. 55579); lower right, *Sympterygia bonaparti*, Müller and Henle (1841), female, from Argentina (U. S. Nat. Mus. No. 53437).

like expansion of the margin of the nostril and is wholly concealed unless the latter be lifted. This character, with the others listed below, sets *D. ommata* so sharply apart from all its relatives that it is necessary to establish for it a third new genus, *Diplobatis.*

FAMILY RAJIDAE

Skates

Two genera of skates are so obviously set apart—the new *Cruriraja* by its pelvic fins and *Dactylobatus* Bean and Weed (1909) by the spatulate extension of the outer margin of each of its pectoral fins—that there is no danger of confusing them with any other known members of their family. The great majority of the remaining rajids—and they are many—fall in two categories as regards the degree of development of the rostral cartilage:

A. Those in which the rostral projection from the front of the cranium extends beyond the tips of the anterior radials of the pectoral fins, very nearly to the tip of the snout;

B. Those in which the rostral cartilage is either nonexistant or only very faintly indicated, and in which the snout region is supported by the forward extension of the pectoral rays on either side, aided more or less by ligamentous bands or sheets reaching forward from the anterior face of the cranium.

The species in category A (with rostral cartilage extending beyond pectoral rays) are so many, and those from different seas so closely resemble one another in many cases, that it would be a boon to students of fishes of the sea bottom if they could be grouped generically by any criteria that would be easy to see or to feel and at the same time give reasonably sharp alternative characters. However, all of the characters that have been proposed for this purpose, such as length and shape of snout, presence or absence of caudal fin-membrane, relative positions of dorsal fins on the tail, spination, and structures of claspers in adult males, have proved to intergrade so completely that there seems no escape from referring all the known members of this group to the old genus *Raja* of Linnaeus (1758).

The members of category B (*i. e.*, either those in which the rostral projection from the cranium is lacking altogether, [Fig. 2, upper and lower right] or in which it is represented by a very slight elevation only [Fig. 2, lower left]) are perhaps separable with reasonable sharpness into two genera, *Sympterygia* Müller and Henle (1841) and *Psammobatis* Günther (1870), according to the degree of concavity of the outer margins of the pelvics, as indicated in the following key. But critical intercomparison, especially of longer known species with those recently

described from Peru (Hildebrand, 1946: 82), may prove that complete gradation exists between these extremes, in which case the older name *Sympterygia* will have precedence.

The Cuban collection now reveals the existence of a third category of typical skates, which includes several small species in which the rostral cartilage, while definitely developed, falls short of the tips of the pectoral rays (Fig. 2, upper left) and hence falls shorter still of the tip of the snout. Examination of the Museum of Comparative Zoology collections shows that *Raja plutonia* Garman (1881, 236; 1913: 335, pl. 18, fig. 1) from the upper part of the Continental Slope in the offing of South Carolina also falls in this category in respect to its rostral cartilage. In fact, Garman, in his original account of this species, remarked that the rostral cartilage did not extend to the end of the snout.

Furthermore, we have yet to see a skate, large or small, fresh or preserved, or from whatever ocean, that cannot readily be referred to one or the other of these three categories. The presence or absence of a rostral cartilage, and its length relative to the pectoral rays if present, is easily determined by touch and, in most cases, by viewing it against a strong light; such examination is possible even for large specimens, while x-ray photographs are even more revealing. Such being the case, we now propose for this category with short rostral cartilage the new genus *Breviraja*.

Key to Genera of Rajidae

1a. Middle rays of pectorals prolonged as spatulate extensions of disc.
Dactylobatus Bean and Weed (1909).

1b. Middle rays of pectorals not prolonged.

2a. Anterior lobes of pelvics in the form of slender, limb-like structures, entirely separate, externally, from the posterior lobes, and arising independently from the lower surface of disc. *Cruriraja*, gen. nov., p. 549.

2b. Anterior lobes of pelvics fin-like (as are the posterior lobes) and continuously connected with the posterior lobes along outer margin of fin.

3a. Anterior face of cranium with a definite rostral process, longer or shorter.

4a. Tip of rostral process extending forward beyond level of tips of anterior rays of pectorals very nearly to extreme tip of snout.
Raja Linnaeus (1758).

4b. Tip of rostral process falling short of level of tips of anterior rays of pectorals, and falling shorter still of extreme tip of snout.
Breviraja, gen. nov., p. 558.

3b. Anterior face of cranium without a definite rostral process, or at most with only a very slight elevation, or even concave in some cases.

5a. Outer margins of pelvics so deeply concave that the fins are divided. *Psammobatis* Günther (1870).[4]

5b. Outer margins of pelvics only very weakly concave, the fins not divided. *Sympterygia* Müller and Henle, 1841.

Cruriraja,[5] Gen. Nov.

Generic characters. Rajidae with outer margin of pelvic so deeply notched that the anterior division is entirely cut off from the remainder of the fin, thus forming a separate limb-like structure that arises independently from the lower surface of the disc some little distance inward from the edge of the disc; inner posterior margin of pectoral continuous with anterior margin of posterior division of pelvic. Anterior division of pelvic subcylindrical, slender, tapering toward the tip, stiff proximally but softer distally, of three articulated segments, with the stoutness of its musculature toward the base suggesting considerable powers of movement; its support is given by the first stout radial and the succeeding two or three slender radials, all of which are articulated to the pelvic arch. Posterior lobe of pelvic fin-like, supported by about 18 radials only, the gap resulting from the loss of the anterior two or three radials that are ordinarily borne along the anterior part of the basipterygial cartilage corresponds in position to the interspace seen, externally, between the anterior and posterior subdivisions of the pelvic fin. Characters otherwise as in *Raja*.

The function of the limb-like specialization of the anterior part of the pelvic fin is not known. It may be tactile, as are the feeler-like pelvics of the hakes of the gadoid genus *Urophycis*, or it may assist in the progress of its owner over the bottom.

Type species. *Cruriraja atlantis* Bigelow and Schroeder (p. 550), the type specimen, Harv. Mus. Comp. Zool., No. 36320; Atlantis Station 3468, Lat. 23° 11′ N, Long. 81° 23′ W, off the north central coast of Cuba; 375 fathoms.

Key to Known Species of *Cruriraja*

1a. Interspace between 1st and 2nd dorsal fins at least 1.5 times as long as base of 1st dorsal. *atlantis*, sp. nov., p. 550.

1b. Interspace between 1st and 2nd dorsal fins not more than about half as long as base of 1st dorsal.

[4] *Malacorhina* Garman (1877) is clearly a synonym of *Psammobatis*, as pointed out by Regan (1914: 22) and by Norman (1937: 33). This appears to apply equally to *Irolita* Whitley, 1931.

[5] From the latin *crus*, a leg or limb, and *Raja*, the generic name of the typical skates.

2a. Large thorns on head and from posterior part of disc out along tail, but no large thorns along midbelt of back between levels of spiracles and outer corners of pectorals. *poeyi*, sp. nov., p. 555.

2b. Large thorns in an unbroken series along midline of back from close behind level of spiracles rearward along disc and tail.

3a. A group of thorns on tip of snout, others along anterior half of rostral ridge, and two thorns in the interspace between the two dorsal fins. *parcomaculata* Bonde and Swart (1924). Off Natal Coast, S. Africa; 298 fathoms.

3b. No thorns on tip of snout, along rostral ridge, or in the interspace between the two dorsals. *durbanensis* Bonde and Swart (1924). Off Natal Coast, S. Africa; 420 fathoms.

Cruriraja atlantis, sp. nov.

Figures 3, 4

Distinctive Characters. The complete subdivision of its pelvic fins separates *C. atlantis* from other known members of the family Rajidae except for its genus mates *C. poeyi*, *C. parcomaculata* and *C. durbanensis;* and the great width of the interspace between its first and second dorsal fins marks it off from all three of these species. The fact that the upper surface of its disc is nearly uniformly covered with small prickles further separates it from *poeyi;* the rounded outer corners of its disc distinguish it from *parcomaculata;* and the several rows of enlarged thorns on its tail separate it from *durbanensis*, which has a single row from nuchal region to first dorsal when young and a single row falling short of first dorsal in older examples.

Description. Proportional dimensions in per cent of total length. Female, type, 332 mm. long, with disc 175 mm. wide. Harv. Mus. Comp. Zool. No. 36320.

Disc: length 40.7; breadth 52.7.

Snout length in front of: orbit 9.5; mouth 12.3.

Orbits: longest diameter 5; breadth between 2.6.

Spiracles: length 2.6; breadth between 6.3.

Mouth: breadth 5.6.

Nostrils: breadth between 5.1.

Gill openings: distance between 1st 11.9; 5th 6.6; lengths 1st 1.1; 3rd 1.3; 5th 1.0.

Distance: snout to cloaca (middle) 38.0; cloaca (middle) to tip of tail 62.0.

First dorsal fin: vertical height 2.4; length of base 3.6.

Second dorsal fin: vertical height 1.8; length of base 3.8.

Interspace between: 1st and 2nd dorsals 9.0; 2nd dorsal and tip of tail 4.4.

Pelvics: length of anterior margin 9.0.

Disc 1.3 times as broad as long, its anterior angle (tip of snout to level of anterior margins of orbits) about 94°, the anterior margins very slightly sinuous, weakly convex opposite orbits; the outer posterior and inner margins gently convex, the outer corners narrowly rounded, the axis of greatest breadth 70% of distance rearward from tip of snout toward axils of pectorals. Rostral cartilage narrow, extending nearly to tip of snout. Pectoral rays terminating anteriorly halfway between orbits and tip of snout. Snout sharp-tipped, its length in front of orbits 1.9 times as long as orbit, its length in front of mouth 2.4 times as long as distance between nostrils. Orbit twice as long as interorbital space and as length of spiracle. Mouth very slightly curved, without a noticeable bow in center. Posterior margin of nasal curtain weakly and irregularly fringed, the outer posterior margin of nostril smooth. Distance between inner ends of 5th pair of gill openings 1.3 times as great as distance between nostrils.

Teeth in 42 series in upper jaw, probably the same in lower, arranged in quincunx, with a low and rather blunt median cusp.

Anterior lobe of pelvic (entirely separated from posterior lobe) fleshy, limb-like, slightly longer than posterior lobe, with two radials besides the first stout one, which is of three segments. Posterior lobe continuous with pectoral, with 18 radials, its outer margin slightly wavy and moderately convex, inner margin straight or slightly concave. Tips of pelvics angular, extending back about ¼ the distance from axils of pectorals toward 1st dorsal.

Tail slender, 1.1 times as long from center of cloaca to origin of 1st dorsal as from tip of snout to cloaca, 1.4 times as long to 2nd dorsal, and 1.6 times as long to tip. First and 2nd dorsals similar in shape and about equal in size; interspace between 1st and 2nd dorsals 2.5 times as long as base of 1st dorsal. Base of 2nd dorsal about as long as base of 1st dorsal; distance from rear end of base of 2nd dorsal to origin of caudal fin-membrane about ½ as long as base of 2nd dorsal; distance from 2nd dorsal to tip of tail slightly greater than length of base of 2nd dorsal. A membranous fold, low down on side of tail, originates anterior to 1st dorsal by a distance about equal to base of latter, very narrow anteriorly, gradually widening rearward to maximum breadth opposite origin of 2nd dorsal and to tip of tail.

Entire upper surface of disc thickly and evenly set with small prickles, except for extreme tip of snout and a narrow band along outer posterior margin of each pectoral. Somewhat larger prickles

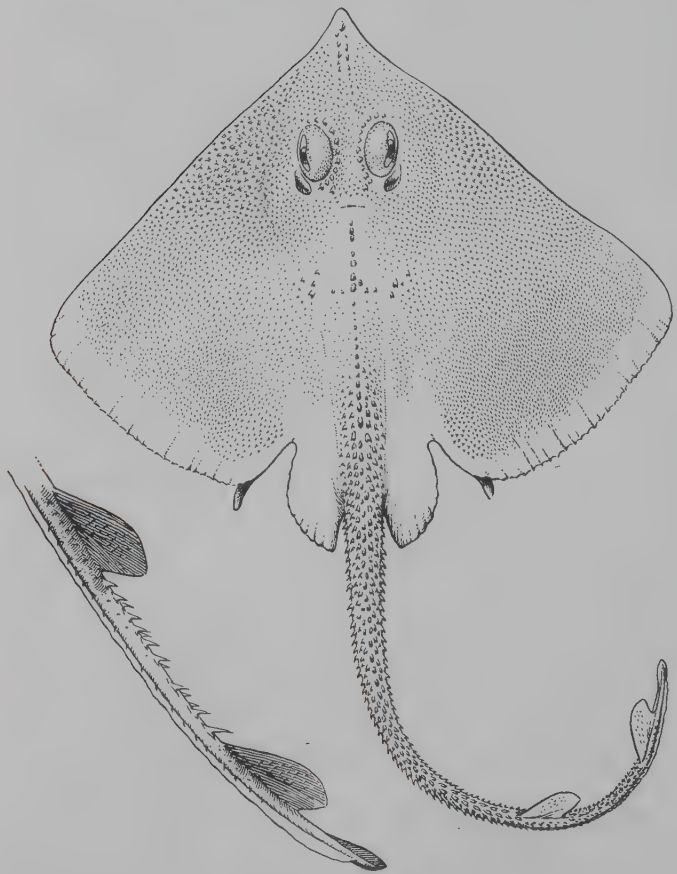

Figure 3. *Cruriraja atlantis*, sp. nov., female, type 332 mm. long (Harv. Mus. Comp. Zool. No. 36320), × 0.6. Dorsal fins and caudal fin membrane, × 1.2.

in the area opposite orbits, mostly with stellate bases so close together as to almost touch. Skin over eyes also prickly. Two or three rows of thorns on anterior part of rostral process. Inner margin of eye with an uninterrupted row of 11 thorns, besides 1 thorn posteriorly toward median line of back. Two or 3 low stout thorns on each scap ula

region. Midbelt of disc with a median row of 7 from nuchal region to pectoral girdle, followed by several very small thorns posterior to latter, increasing in size rearward. Also 1 or 2 additional rows of thorns on either side of middle row from a little in advance of axils

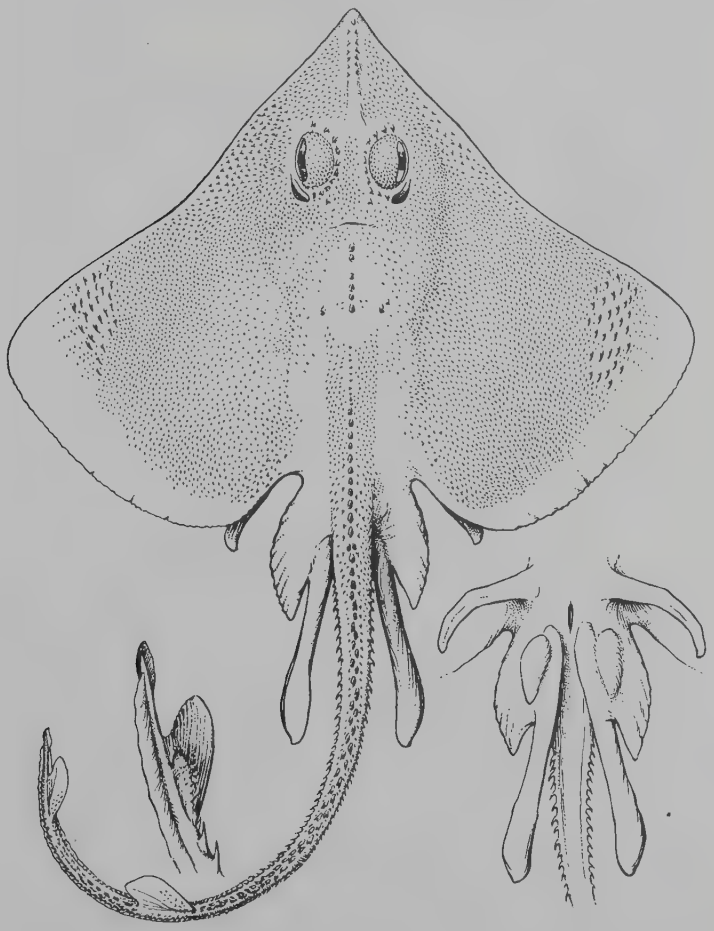

Figure 4. *Cruriraja atlantis*, sp. nov., male, 297 mm. long (Harv. Mus. Comp. Zool. No. 36321), × 0.7. Pelvic fins and claspers, × 0.7; second dorsal fin and caudal fin membrane, × 1.5.

of pectorals. Tail very thorny above and on sides, with 6 or 7 rows along anterior part, but with only 2 or 3 rows approaching the 1st dorsal; 1 or 2 rows between dorsals, succeeded by smaller prickles along sides of tail to a point opposite rear end of base of 2nd dorsal. Dorsals with a few prickles. Pelvics smooth. Lower surface of disc and tail smooth.

Color. Upper surface uniformly pale brown; disc without definite markings; a dusky band on the tail in the region of each dorsal fin; the dorsals black (a very conspicuous feature), as is the caudal. Lower surface whitish or yellowish, the abdomen and posterior parts of pectorals irregularly blotched with dark brown, the posterior lobes of the pelvics still darker brown.

Additional Specimens. A mature male, 297 mm. in total length and 161 mm. wide, with a small patch of alar thorns on each pectoral, differs from the female as follows: The anterior margins of the disc are concave opposite spiracles; the mouth is somewhat more curved; the outer posterior nasal margin has a few very short fringes; the posterior lobes of the pelvics are narrower and their tips more pointed; the tail has fewer thorns, for it lacks the rows immediately beside the median one. The lower surface of the disc is plain yellowish on the anterior half, pale dusky brownish on the posterior half, with an irregular demarkation separating the two areas; the anterior lobes of the lower surfaces of the pelvics are darker than in the female.

An immature male, 160 mm. long with disc 85 mm. wide, closely resembles the larger specimens except that the anterior margins of the disc are not noticeably concave opposite the spiracles. However, on a very young male, only 125 mm. long with disc 62 mm. wide, the pectorals are bare of prickles, although the midzone of the back is already prickly from the scapular region to opposite the tips of the pelvics; only 4 or 5 thorns have yet developed around the inner margin of each orbit. On the disc the median row of thorns is represented by only 2 or 3, these widely spaced, between nuchal region and level of axils of pectorals; these are succeeded by 1–2 rows of long sharp thorns rearward to the first dorsal, and between the dorsals. Color below plain whitish.

Developmental Stages. Nothing is known except that the new-born are about 100 mm. in total length.

Size. The largest specimens taken were a female 332 mm. long and a mature male 297 mm. Our collection contains 12 specimens, nine males and three females, 100 to 332 mm. in total length, with discs 50 to 175 mm. wide.

Habits. This is a deep-water species, all the specimens thus far having been taken in depths of 280 to 425 fathoms.

Range. Known only from off the north central coast of Cuba.

Cruriraja poeyi, sp. nov.

Figures 1, 5

Distinctive Characters. The pelvic fins of *C. poeyi* make it separable at a glance from all other members of the family Rajidae yet known from the western Atlantic, except for *C. atlantis.* It differs from the latter in the facts that the upper surface of its disc is largely smooth excepting around the eyes and snout and along the mid-dorsal zone posterior to the scapular region, and furthermore, its two dorsal fins are close together. The smoothness of the disc also separates it from *C. parcomaculata* and *C. durbanensis* from South Africa, which are more or less covered with small spines in addition to the enlarged median and orbital thorns.

Description. Proportional dimensions in per cent of total length. Female, type, 328 mm. long, with disc 208 mm. wide. Harv. Mus. Comp. Zool No. 36324.

Disc: length 48.2; breadth 63.5.

Snout length in front of: orbit 12.2; mouth 14.0.

Orbits: longest diameter 5.2; breadth between 3.3.

Spiracles: length 2.7; breadth between 7.9.

Mouth: breadth 7.0.

Nostrils: breadth between 6.4.

Gill Openings: distance between 1st 13.7; 5th 7.6; lengths 1st 1.4; 3rd 1.5; 5th 1.0.

Distance: Snout to cloaca (middle) 42.7; cloaca (middle) to tip of tail 57.3.

First dorsal fin: vertical height 1.8; length of base 4.0.

Second dorsal fin; vertical height 1.8; length of base 4.6.

Interspace between: 1st and 2nd dorsals 1.2; 2nd dorsal and tip of tail 4.0.

Pelvics: length of anterior margin 12.5.

Disc 1.3 times as broad as long, its anterior angle (tip of snout to level of anterior margins of orbits) 98°, the anterior margins slightly sinuous, being weakly convex opposite anterior part of orbits, the outer corners narrowly rounded, the posterior margins weakly convex, the posterior corners broadly rounded, the inner margins nearly straight, and the axis of greatest breadth 67% of the distance back from the snout toward axils of pectorals. Rostral process very narrow, reaching

tip of snout, the anterior rays of pectorals falling well short. Snout pointed, its length in front of orbits 2.3 times as long as orbit, its length in front of mouth 2.2 times as long as breadth between nostrils. Orbit 1.6 times as long as distance between orbits and 1.9 times as long as spiracle. Mouth nearly straight. Nasal curtain fringed with a few very short knob-like lobes, the outer posterior margin of nostril smooth. Distance between inner ends of fifth gill openings 1.2 times as long as between nostrils.

Teeth in $\frac{46}{44}$ series, close set, in quincunx, circular at base, with a low triangular cusp pointing inward excepting near corners of mouth

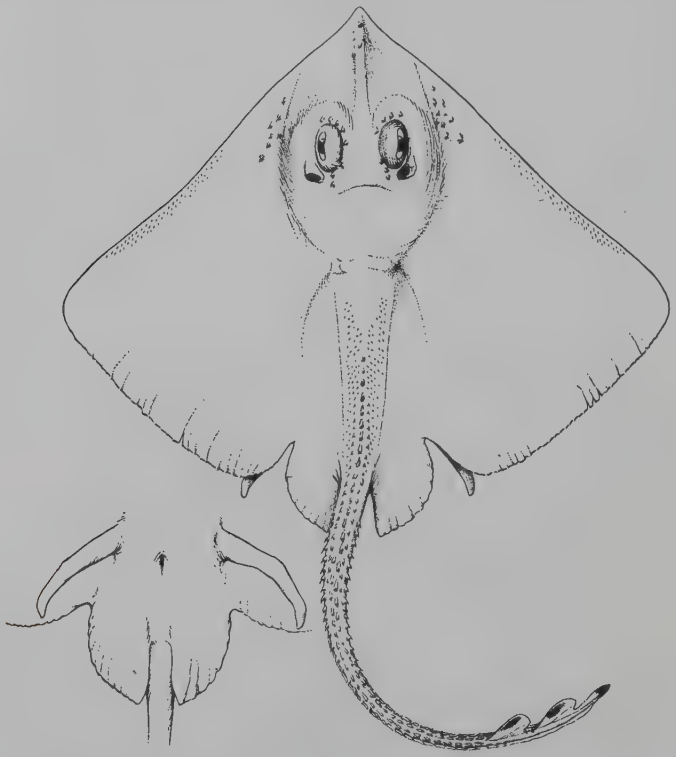

Figure 5. *Crurraja poeyi*, sp. nov., female, type, 328 mm. long (Harv. Mus. Comp Zool. No. 36324), × 0.5. Pelvic fins, × 0.5.

where cusps are usually lacking; the anterior rows worn nearly smooth.

Anterior lobe of pelvics about as long as posterior lobe. Outer margin of posterior lobe broadly rounded, its edge weakly scalloped, the inner margin nearly straight. Tips of pelvics moderately pointed, extending back about ¼ the distance from axils of pectorals toward 1st dorsal.

Tail narrow, its length from center of cloaca to 1st dorsal equal to length from snout to cloaca, 1.1 times to 2nd dorsal, 1.3 times to tip. Dorsals close together, the interspace about ⅓ as long as base of 1st dorsal, which is about equal to base of 2nd and to length of caudal fin. A narrow membranous fold, beginning low down on each side of tail, extends from about midway between tips of pelvics and origin of 1st dorsal to opposite the middle of caudal; widest opposite dorsals.

Upper surface of disc prickly over a narrow band along anterior margins from opposite the middle of orbits nearly to outer corner of disc, and along mid-dorsal ridge from a little posterior to pectoral girdle rearward. A small patch of thorns near end of rostral ridge, 7 or 8 between orbit and margin of disc; 8 on one side and 7 on the other along inner margin of orbit, the series interrupted about midway; also, a median row extending rearward from about midway between pectoral girdle and level of axils of pectorals, flanked by 2 or 3 rows of smaller thorns from a little anterior to axils of pectorals. Otherwise naked, including skin over eyes. Tail conspicuously rough; 6–7 rows of thorns anterior to tips of pelvics, although no one row is exactly in the midline, and 4 rows posteriorly, the anterior tail thorns more closely spaced than those rearward; 2 pairs of opposing thorns between dorsals. Dorsals prickly, but caudal and pelvics smooth. Lower surface smooth.

Color. Upper surface pale coffee brown except for a translucent area on either side of rostral cartilage; anterior parts of dorsals and tip of caudal membrane black. Lower surface of disc of about same shade as above, somewhat mottled with paler and darker, with pale areas around the mouth and along the gill openings. Tail paler than disc.

Additional Specimens. A male, 327 mm. in total length with disc 197 mm. wide, differs from the female chiefly as follows: Anterior angle of disc more acute (86°); snout sharper; posterior margin of nasal curtain conspicuously fringed on one side but almost smooth on the other; teeth in 50 series in upper jaw, with longer and sharper cusps; pelvics narrower, with tips more pointed; claspers well developed, extending beyond tips of pelvics a distance equal to width of mouth; a

somewhat larger patch of malar thorns beside the orbits and a triangular patch of alar thorns on the outer parts of pectorals.

Several medium-sized specimens, 230 to 260 mm. long, with color better preserved, have roundish spots somewhat darker than the ground color; these are about half as large as the orbit and are scattered on the disc posterior to the spiracles, except along the outer posterior margins. A newborn specimen, 83 mm. in total length with disc 49 mm. wide, has a single median row of thorns from a little in advance of the axils of pectorals to the 1st dorsal. Seemingly these are lost with growth, and are replaced by one row on each side of the midline. There is also a single row low down on each side of the tail and a patch of prickles in the midzone from a little in advance of the axils of pectorals to a little posterior to the tips of the pelvics.

Developmental Stages. Nothing is known except that this skate, when newborn, is about 90 mm. in total length and closely resembles the adult.

Size. The largest specimen obtained was 328 mm. in total length. A male of about this size had well developed claspers, hence the total length reached by this species is probably not much greater than 400 mm. The collection contains 15 specimens, six males and nine females, 83 to 328 mm. long and 49 to 208 mm. wide; of these, 13 were trawled by the research vessel ATLANTIS and one by the U. S. Fisheries vessel ALBATROSS.

Habits. All specimens thus far known have been trawled in depths ranging from 210 to 475 fathoms, on hard sandy bottom.

Range. Known from off the north central and southwest central coasts of Cuba and off St. Augustine, Florida.

Breviraja, GEN. NOV.[6]

Rajidae with a rostral cartilage, but with the latter falling considerably short of the extremities of the anterior rays of the pectorals and hence short of the tip of the snout; the anterior pectoral rays of the two sides are either close together anteriorly or are farther separated. Characters otherwise as in *Raja*.

Type species, *Breviraja colesi* Bigelow and Schroeder, sp. nov.

Only one of the many species of the family previously described (*i. e.*, the *Raja plutonia* of Garman [1881]) is known with certainty to fall in this new genus. But the Cuban collections of the ATLANTIS include several new species that belong here, one of which is described below as type of the genus; the description and naming of the others will be postponed until a later occasion.

[6] From the latin "brevis," and *Raja*, the generic name of typical skates.

Breviraja colesi, sp. nov.

Figures 2 (upper left), 6

Distinctive Characters. Two characters, namely the lack of enlarged thorns in the mid-dorsal belt of the disc between the scapular region and the pelvic girdle, and a coloration which includes brownish roundish spots (some spots on the adult having pale centers), set off *B. colesi* from *B. plutonia* (Garman 1881), the only other skate yet described from the western Atlantic with pectoral rays extending forward beyond the rostral process.

Description. Proportional dimensions in per cent of total length. Female, type, 333 mm. long, and 160 mm. wide. Harv. Mus. Comp. Zool. No. 36374.

Disc: length 45.9; breadth 48.0.

Snout length in front of: orbit 9.8; mouth 11.2.

Orbits: longest diameter 4.5; breadth between 3.0.

Spiracles: length 2.8; breadth between 5.7.

Mouth: breadth 6.3.

Nostrils: breadth between 6.6.

Gill openings: distance between 1st 13.6; 5th 6.6; lengths 1st 1.8; 3rd 1.8; 5th 1.5.

Distance: snout to cloaca (middle) 41.4; cloaca (middle) to tip of tail 58.6.

First dorsal fin: vertical height 1.5; length of base 3.6.

Second dorsal fin: vertical height 1.5; length of base 3.6.

Interspace between: 1st and 2nd dorsals 0.0; 2nd dorsal and tip of tail 1.5.

Pelvics: length of anterior margin, 10.2.

Disc 1.05 times as broad as long, its anterior angle (snout to level of anterior end of rostral process) 135°, the anterior margins, outer corners, outer posterior margins, posterior corners and inner margins of disc all rounded, the outer corners most broadly so, the axis of greatest breadth 70% of the distance back from tip of snout toward axils of pectorals. Rostral process short, triangular, forming an angle of 40° (x-ray), extending rigidly for only ⅔ of the distance from center of mouth toward tip of snout. Pectoral rays extending forward well in advance of rigid rostral process. Snout blunt, with a small protuberance at tip, its length in front of orbits 2.16 times as long as orbit, its length in front of mouth 1.7 times as long as distance between nostrils. Orbit 1.5 times as long as distance between orbits and 1.6 times as long as spiracle. Mouth bowed centrally. Posterior margin

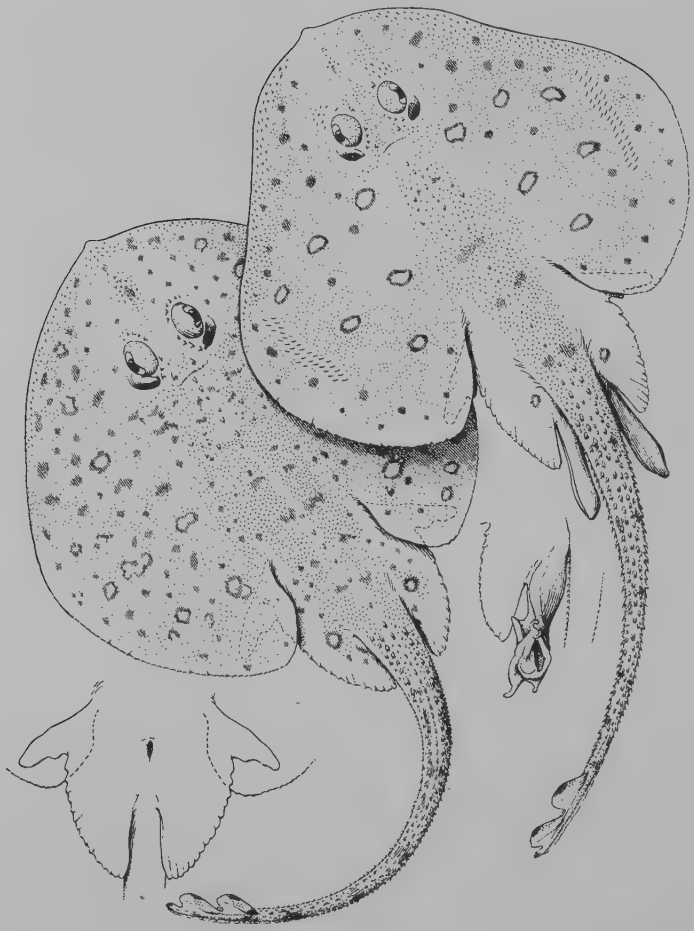

Figure 6. *Breviraja colesi*, sp. nov., female, type, 333 mm. long, and pelvic fins (Harv. Mus. Comp. Zool. No. 36374). Male, 320 mm. long (Harv. Mus. Comp. Zool. No. 36447) and clasper of a mature male; all × 0.5.

of nasal curtain prominently fringed, the outer posterior margin of nostril finely so. Distance between 5th gill openings equal to distance between nostrils.

Teeth in 50 series in upper jaw, probably about the same in lower, close set, in quincunx, with a very small cusp on an ovate base.

Pelvics deeply notched, the anterior lobe with two radials besides the first stout one, which has three segments, its posterior margin slightly wavy, its anterior margin about ⅔ as long as distance from origin of pelvic to rear tip of lobe; the posterior lobe with 24 radials, its outer margin weakly scalloped and moderately convex, its inner margin nearly straight. Tips of pelvics narrowly rounded, extending back about ⅜ of the distance from axils of pectorals toward 1st dorsal.

Tail slender, its length from center of cloaca to origin of 1st dorsal 1.2 times as long as from tip of snout to cloaca, its length to 2nd dorsal 1.3 times and to tip 1.4 times. Dorsals confluent, the base of 1st dorsal as long as base of 2nd. Length of caudal membrane about ⅖ as long as base of 2nd dorsal. A thin and narrow lateral fold, originating on each side of tail a little beyond tips of pelvics, widens somewhat posteriorly and continues to extreme tip.

Upper surface of disc, including skin over eyes, rough with small close-set prickles except at margins around posterior angles where they are sparse. A narrow band of very small thorns (slightly larger than the prickles) along anterior margin from level of spiracles forward; a patch of small thorns over end of rostral process about ⅔ of distance from orbits toward tip of snout; inner margin of orbit to spiracle with 10 or 11 thorns, the row interrupted opposite middle of orbit; a median pair of thorns on nuchal region a little posterior to spiracles; 4 or 5 small thorns on each scapular region. An interrupted row of small thorns along midline of back—6 from the nuchal region to pectoral girdle, 6 more widely spaced to the level of the axils of pelvics, followed by 44 more closely crowded and less regularly arrayed along the tail to the origin of the 1st dorsal. Each side of tail with 2 or 3 irregular rows of larger thorns that become increasingly crowded rearward, and with smaller thorns extending from the level of 1st dorsal to the tip. Dorsals prickly on anterior half or ⅔ of fins. Pelvics with a few small prickles on central part of posterior lobe. Disc and tail smooth below.

Color. Upper surface of disc pale brown mottled with numerous irregular spots and blotches of darker brown, its outer part also with a variable number of larger roundish spots with pale centers and brown margins, one being situated on the center of each posterior pelvic lobe. Tail with various pale brown markings, some appearing as faint crossbars, its lateral membranous folds whitish. Upper

anterior part of each dorsal and anterior base of 1st dorsal with a bronze blotch. Lower surface of disc and of tail pale yellowish or whitish.

Additional Specimens. An immature female 150 mm. long has only 5 or 6 thorns around the inner margin of the orbit, 3 median thorns from the nuchal region to the pectoral girdle, and one only over each scapular region; the thorns on the tail are in more regular rows than in the adult female, and there are 7 or 8 obscure cross bars on the tail. A mature male 320 mm. long has the anterior margin of the disc slightly concave opposite and posterior to the spiracles, the outer angle of the pectorals are more broadly rounded and the tips of the pelvics are more narrowly rounded than on the female; also the tail is longer (1.6 times as long from center of cloaca to tip as from snout to cloaca). The outer margins of the disc opposite and in front of the orbits are armed with malar thorns, slightly larger than the prickles, and there are 2 to 3 rows of alar spines near the outer angles of the pectorals, the extreme length of the rows being a little greater than the distance between the outer ends of the spiracles. The male resembles the female in general coloration, but it has fewer blotches and spots and lacks the blotch at the base of the first dorsal.

Developmental Stages. Nothing is known except that a very young specimen, with disc only 43 mm. wide, bears a close resemblance to the adults.

Size. This species apparently does not reach a length of more than 400 mm., the largest female taken being 333 mm. long, while a mature male was only 320 mm. We have eight specimens of this species, four males and four females, 80 to 333 mm. in total length, with discs 43 to 160 mm. wide, all trawled by the research vessel ATLANTIS.

Habits. All specimens thus far known have been trawled in depths ranging from 200 to 285 fathoms.

Range. Known from Cochinas Bay on the south coast of Cuba, and off Matanzas and Santa Clara Provinces of the north coast.

FAMILY TORPEDINIDAE

ELECTRIC RAYS WITH TWO DORSAL FINS

Diplobatis, GEN. NOV.[7]

Figures 7, 8 (right), 9

Generic characters. Torpedinidae with each nostril subdivided about midway of its length into two separate apertures by a cross bridge of

[7] διπλοος, double, referring to the structure of the nostril, and βατις, a skate or ray.

stiff tissue; outer aperture exposed but the inner entirely roofed over by the joint nasal curtain. *Diplobatis* falls with *Narcine* in most of its other characters; *i. e.*, narrow protractile mouth with labial cartilages at the corners, normally developed eyes with rather prominent orbits, relatively long tail with lateral folds, pelvics entirely separate one from the other and free from the sides of the tail at their extreme tips, and nasal curtain much wider than long. However, the relationship of its tooth bands to its thick, fleshy lips affords a second generic charac-

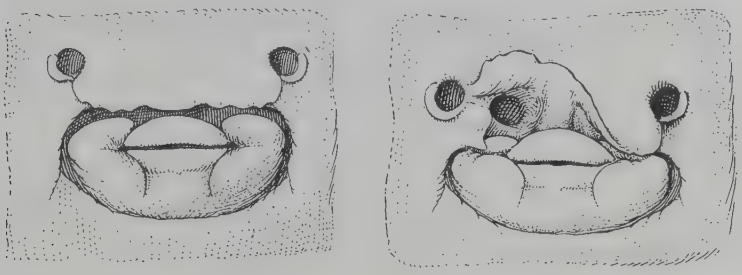

Figure 7. *Diplobatis ommata*, female, about 98 mm. wide; left, mouth and nostril with nasal curtain lifted only enough to show shape of upper lip; right, with right-hand side of nasal curtain rolled back to show the transverse division of the nasal aperture. × 2.75.

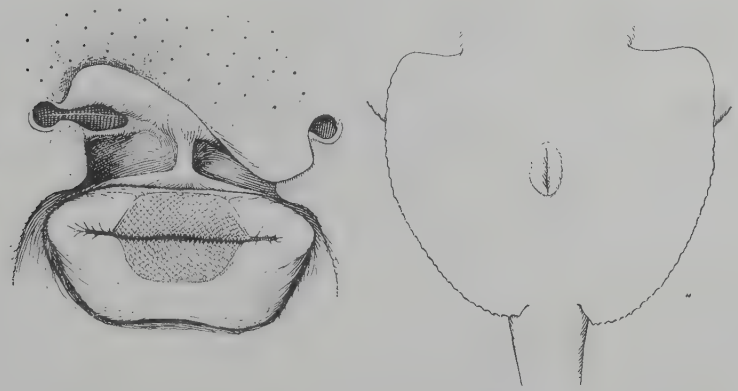

Figure 8. Left, *Narcine brasiliensis*, specimen 218 mm. wide, mouth and nostril with nasal curtain rolled back to show single nasal aperture, and extension of dental bands over the lips, × 1 33; right, *Diplobatis ommata*, ventral view of pelvic fins of female, about 98 mm. wide, × 0.7.

ter; its teeth are entirely concealed when the mouth is retracted and closed, while the median sector of each lip, corresponding in its sidewise extent to the sidewise extension of the tooth bands within the mouth, is marked off at either end by a deep transverse groove when

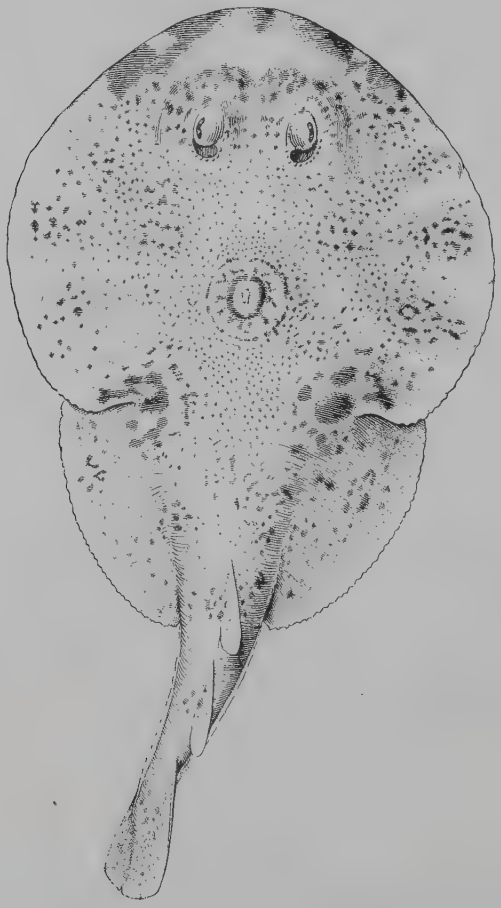

Figure 9. *Diplobatis ommata*, female about 98 mm. wide, to show color pattern

the mouth is retracted. In all other genera of the family in which the mouth is protractile,[8] the tooth bands extend so far forward and the median sectors of the lips are so thin (anteroposteriorly) that several of the anterior rows of teeth are fully exposed even when the mouth is tightly closed. And in them the lips are not crossed by definite transverse grooves corresponding with the lateral limits of the tooth bands, even when the mouth is fully retracted (Fig. 8). The type species is *Discopyge ommata* Jordan and Gilbert (1890), of which *Narcine ommata* Clark (1936) appears to be a synonym; Pacific Coast of America, Gulf of California to Panama.

The color pattern of this interesting little electric ray is so conspicuous and so characteristic that we include a drawing to show it (Fig. 9); see Beebe and Tee-Van (1941, pl. 1, Fig. 2.) for a photograph showing a very similar pattern for a male specimen.

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Contribution No. 451

SOME RECENT DEVELOPMENTS IN THE STUDY OF THE GULF STREAM

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INTRODUCTION

At Cape Hatteras the Gulf Stream leaves the Continental Slope, so that as far as the deep current is concerned its course is no longer confined. The current again approaches the Continental Shelf off Georges Bank and off the Grand Banks, but in neither area does it flow normally along the Continental Slope as a river pressing against its bank. The band of water which separates the Gulf Stream from the Continental Shelf in the sector between Cape Hatteras and the Grand Banks is usually called "slope water." The great body of water to the south and east of the Stream is known as the Sargasso Sea or Central Atlantic water. Although it is not a part of this paper to discuss the physical characteristics and the similarities or dissimilarities of these two masses of water, there is an important difference that must be mentioned. In the slope water, the main thermocline lies much nearer to the surface than it does in the Sargasso Sea. The depth of this thermocline does not gradually change from one body of water to the next but changes abruptly within a relatively short distance. The Gulf Stream occupies this transition belt where the midpoint of the thermocline drops from an average depth of 250 meters in the slope water to an average of 750 meters in the Sargasso Sea.

In the sector between Cape Hatteras and the Grand Banks, the Gulf Stream resembles a "river in the ocean" rather than a current pressed close against the margin of the ocean basin. For some purposes it is more convenient to think of the Gulf Stream as a transition belt or as a boundary phenomenon. The approximate mean position of this boundary, as taken from the U. S. Hydrographic Office chart No. 1412, is shown in Fig. 1. The dots in the figure show where the available subsurface temperature observations have indicated the abrupt change in the depth of the thermocline.

[1] Contribution No. 451 from the Woods Hole Oceanographic Institution.

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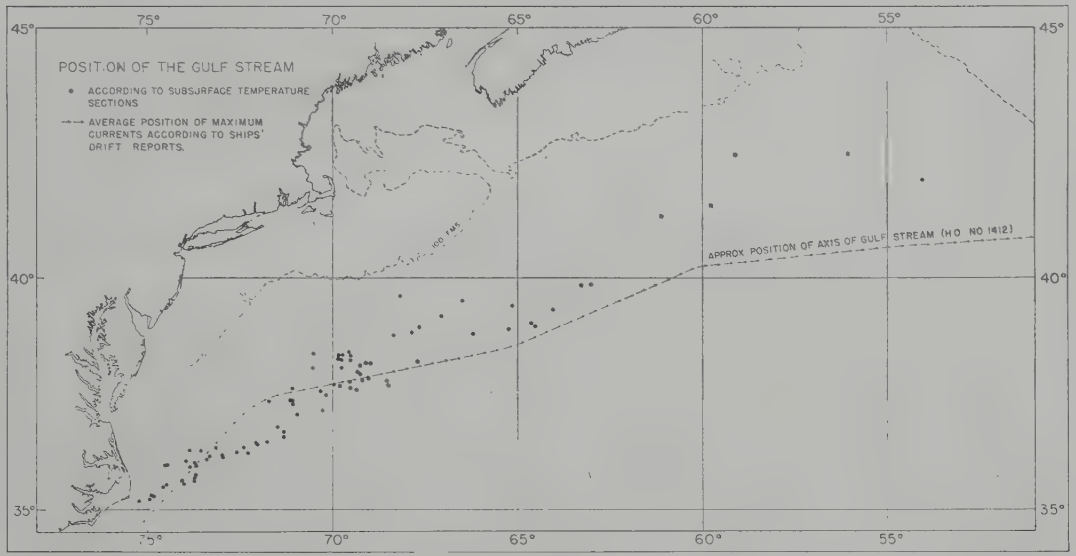


Figure 1. Comparison between the average path of the axis of the Gulf Stream as deduced from ship reports at the U. S. Hydrographic Office (arrows) and cross current temperature profiles (dots).

Our understanding of this part of the Gulf Stream system has come from three quite different sorts of studies, and only recently has a radically new attack on the problem been made. There is, first of all, a long series of studies in which average conditions in and near the Gulf Stream have been shown in various ways. The mean position of the axis of the Stream as given in Fig. 1 is an example. As more data became available, these plottings of the average physical characteristics of the current have been greatly improved, either by shortening the time intervals (Fuglister, 1947) or by combining several different types of information (Neumann and Schumacher, 1944). As will be shown below, although these observations were useful as a preliminary step in understanding the Gulf Stream, all such studies in the process of averaging the available data show the current as being considerably broader and weaker than it actually is at any given time. Of course, the defect has been generally understood by oceanographers, but how pronounced it could be has only recently been demonstrated.

A second general method, which was employed vigorously during the period 1930–1940, was the study of profiles of the Gulf Stream derived from lines of serial temperature and salinity observations. These Gulf Stream sections required only two or three days to complete and thus approached the synoptic ideal, but the interpolations, both vertical and horizontal, were relatively great. Especially when in and near the current, the observer experienced great difficulty in controlling the navigation of the research vessel, and the placing of the stations in relation to the current was always in doubt. This method when used under the most favorable circumstances provided considerable evidence (Iselin, 1940) that in cross section the current behaves just as would be predicted from the circulation theorem. However, because of the relatively wide spacing of the observations, calculations of the velocity could be regarded only as minimum values, and there remained even greater doubt as to the velocity at considerable depths below the surface. The total transport of the current could be computed from such observations with somewhat greater assurance. In these Gulf Stream profiles, marked distortions of the main thermocline layer on either side of the current were encountered. In the absence of reliable surface current observations such undulations of the isotherms could only be tentatively ascribed to eddies. Furthermore, in each case only a single profile was obtained.

At the same time that these subsurface studies were being made, the surface temperature records from commercial ships making regular runs across the area were being obtained. From these data, Church (1937) concluded that the Gulf Stream wandered or meandered to an increasing degree as it moved eastward from Cape Hatteras. Although

the surface temperature alone is not always an exact indication of the location of the swiftest current, this profitable line of study probably was not continued as long as it should have been.

A third approach to the problem of the Gulf Stream has stemmed from theoretical studies. The contribution of the basic ideas in the circulation theorem has already been mentioned. Rossby (1936) pointed out that the Gulf Stream, at least to some extent, must behave as a wake stream and that countercurrents and eddies should be found on both sides of it. More recently Stommel (1948) has contributed much to our understanding of why the great North Atlantic eddy, of which the Gulf Stream is a part, has been found to be so much swifter and narrower in the west than in other sectors. As will be shown below, the new observations are not inconsistent with these various theories, but as might be expected, they present us with a somewhat more complicated picture. It is hoped that in time the theory will be refined to meet the new aspects.

NEW INSTRUMENTS

During the war two new instruments were developed that allowed a different approach to the study of the Gulf Stream. These instruments were the bathythermograph, with which subsurface temperature data can be obtained while a ship is underway, and the loran, which makes it possible to obtain navigational fixes at any hour of the day or night.

With the bathythermograph, a nearly continuous temperature-depth profile can be obtained. Within a few minutes of the time of lowering this instrument, the observer has a clear picture of the temperature structure of the water through which the ship is passing. With this knowledge, he can maneuver the ship so as to remain close to any particular thermal structure that is to be studied. It is true that the instrument shows only the surface layer temperatures, to a depth of 900 feet with the latest model bathythermograph, but as will be shown, it is evident that even in this shallow layer the temperature structure reflects the current pattern.

The loran makes it possible to maneuver a ship in and out of a current over a period of days without becoming hopelessly involved in navigational problems. Unfortunately this does not hold for every portion of the Gulf Stream system. In many areas over the ocean, the loran coverage is poor or nonexistant, but it is fortunate that the coverage is extremely good over the area traversed by the Gulf Stream between Cape Hatteras and Georges Bank. Even in this region, a single loran fix should not be relied on, but if the instrument is in

operation continuously and if fixes are obtained at frequent intervals, the results are far more reliable and useful than the best dead reckoning and celestial navigation.

Other instruments have been and are being developed which will be of value in ocean current studies. For example, there are new electrical means of recording surface salinity, and the multiple sea sampler gives promise of providing practical means of observing the subsurface distribution of salinity at frequent intervals. It is hoped that these devices will be used in future surveys of the Gulf Stream, but since they were not employed in these studies, they are mentioned only briefly.

RECENT INVESTIGATIONS

The first studies of the Gulf Stream made with a bathythermograph were of rather limited scope (Spilhaus, 1940). As the instrument was further developed, a number of sections were run across the Stream, and it became quite clear that the temperature structure in the surface layer (450 or 900 feet) indicated the presence of the current. Fig. 2 shows two such temperature profiles, one made in August 1945 and the other in December 1947. A study of these and other sections shows that the depth of the 65° F. isotherm can be used conveniently to indicate the position of the Gulf Stream as well as large eddies and countercurrents. In the Sargasso Sea, the temperature of the water at a depth of 900 feet is at all seasons of the year between 64° and 65° F. There is no evidence of the water at this depth ever becoming appreciably warmer than this, but on the other hand a strong eddy or current may cause it to become several degrees cooler. In the swiftest portion of the Gulf Stream, the 65° isotherm abruptly moves up to the surface. During the coldest season of the year, all slope water is colder than 65°, while at other times of the year this isotherm is generally less than 200 feet deep. Anticyclonic eddies in the slope water area will cause the 65° isotherm to deepen, but rarely will it go to as great a depth as it occupies in the Sargasso Sea.

In spite of the fact that these temperature profiles are comparatively easy to obtain, only a few complete cross current sections are yet available. Shallow temperature profiles show where a strong current has been encountered, but they alone do not permit any calculations of velocity. With the introduction of the loran, not only was the problem of navigation near a current much simplified, but a means of approximating the velocity of the current at the surface was supplied. The loran data confirmed what had long been suspected on theoretical grounds; namely, that the sharp drop of the isotherms in the surface layer occurs where the current is swiftest.

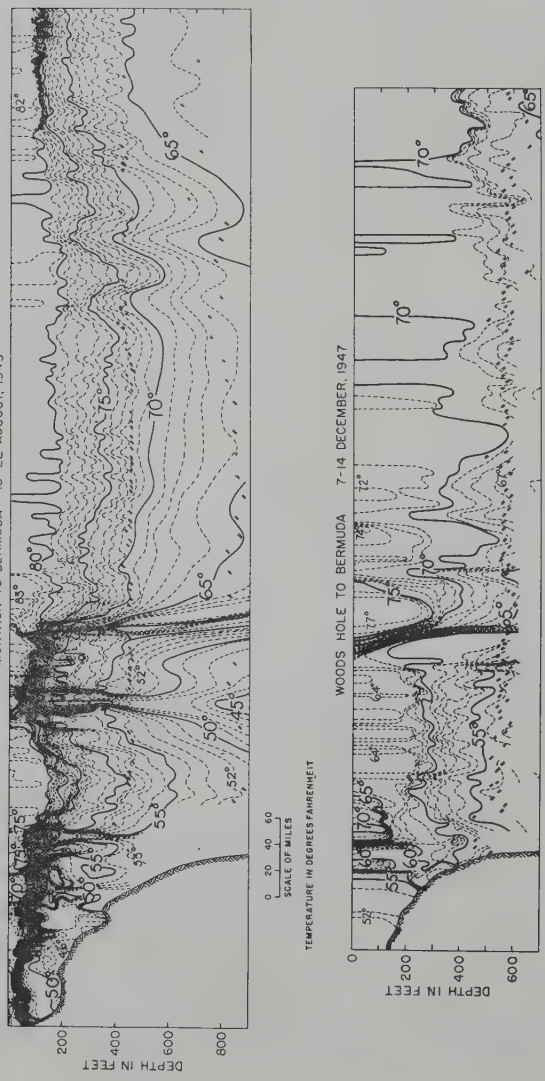


Figure 2. Bathythermograph profiles across the Gulf Stream off southern New England. The diagonal marks indicate the greatest depth achieved on each lowering. In the upper section the 450-foot instrument was used alternately with the 900-foot instrument

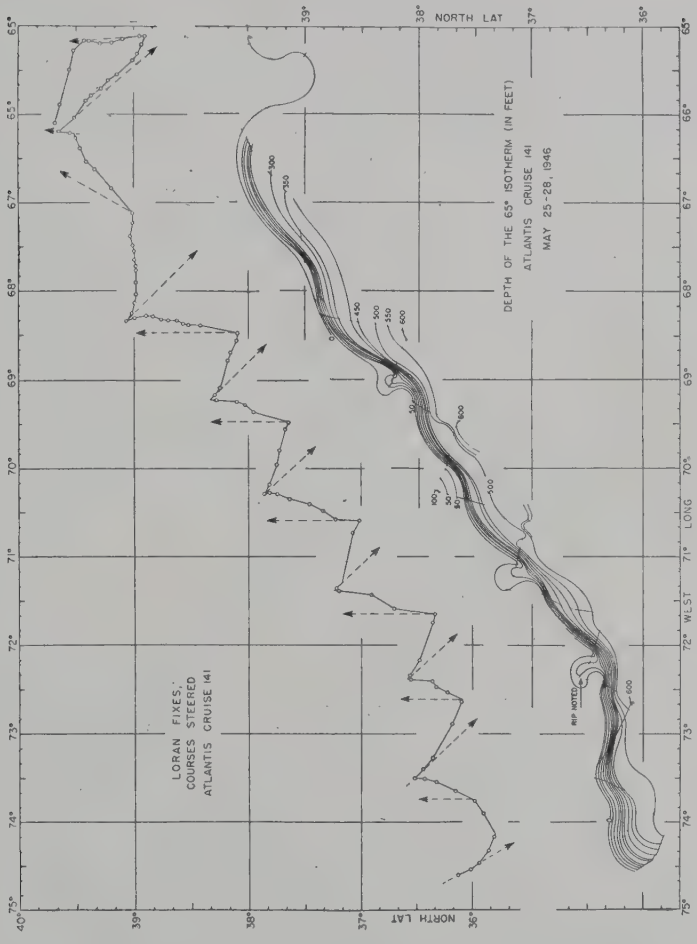


Figure 3. Survey of the northern edge of the Gulf Stream showing the departure between dead reckoning and observed positions (above) and the probable depth contours of the 65° F. isotherm (below).

In May 1946, the two new instruments were used aboard the research ketch ATLANTIS in a new type of survey of the Gulf Stream.[2] Instead of observing an individual section, a series of short sections

[2] This survey, as well as the collection of much of the other data presented here, was carried out under Contract No. N6onr-277 with the Office of Naval Research.

was run, crossing and recrossing the Stream, the ship drifting with the current; in this manner a large area was covered and the course as well as the velocity of the Stream was determined. This series of sections is shown in Fig. 3. The upper portion of the diagram shows the loran fixes and the courses steered, the lower portion shows the slope of the 65° isotherm across the Gulf Stream.

MEANDERINGS OF THE GULF STREAM

The May 1946 cruise of the ATLANTIS agrees with Church's (1937) findings in that the Gulf Stream follows a meandering course after leaving Cape Hatteras. Although only two other short cruises of this type have been made, all of them in the spring of the year, it is apparent at any particular meridian that the Stream may move north or south at the rate of a mile or two a day. At one point, the position of the Stream may be shifted north by 20 miles in about two weeks, while in the same period another part of the Stream may have moved a corresponding distance toward the south. This characteristic of the current makes it impossible to determine by a single section whether or not the Stream as a whole is north or south of its mean position. This point is emphasized, because the north-south migration of the Gulf Stream has been thought to be closely associated with the seasonal variations of the circulation of the North Atlantic.

VELOCITY OF THE GULF STREAM

The data from the May 1946 cruise, and from other more recent cruises of the ATLANTIS, show that the velocity in the swiftest part of the Gulf Stream is generally between four and five knots. Such high velocities are usually confined to a relatively narrow band 10 to 15 miles wide situated near the inshore or left-hand edge of the current. A number of these calculations of current velocity and direction are plotted in Fig. 4. These calculations and others obtained recently show not only that the highest velocities in the Gulf Stream are greater than most previous estimates, but that currents associated with the eddies both north and south of the Stream are surprisingly strong. The relatively fast (3 knot) currents of these eddies would not often be noticed in general navigation, since for each current moving in one direction there is an opposite current of equal, or nearly equal, velocity near by. It is for this same reason that when crossing the Gulf Stream the ships' drift records show the velocity as less than it actually is. The countercurrents near the Stream are usually indistinguishable from the main flow in the navigational record. Because of the meanderings, eddies and countercurrents which are characteristic of the

Gulf Stream area, it would be difficult for a ship to maintain a course so that it would remain in the swiftest, eastward flowing, portion of the current. Drift records, based on infrequent celestial fixes from a ship following the mean course of the Gulf Stream, would almost certainly not show the maximum velocity of the current. Recently the ATLANTIS spent 36 hours investigating a 3- to 4-knot countercurrent near

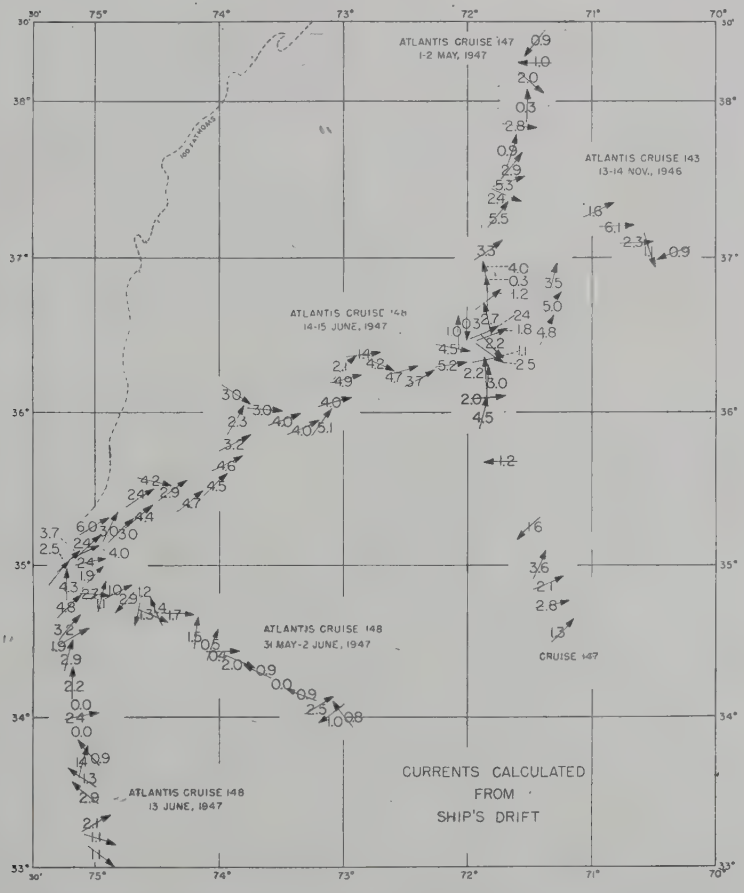
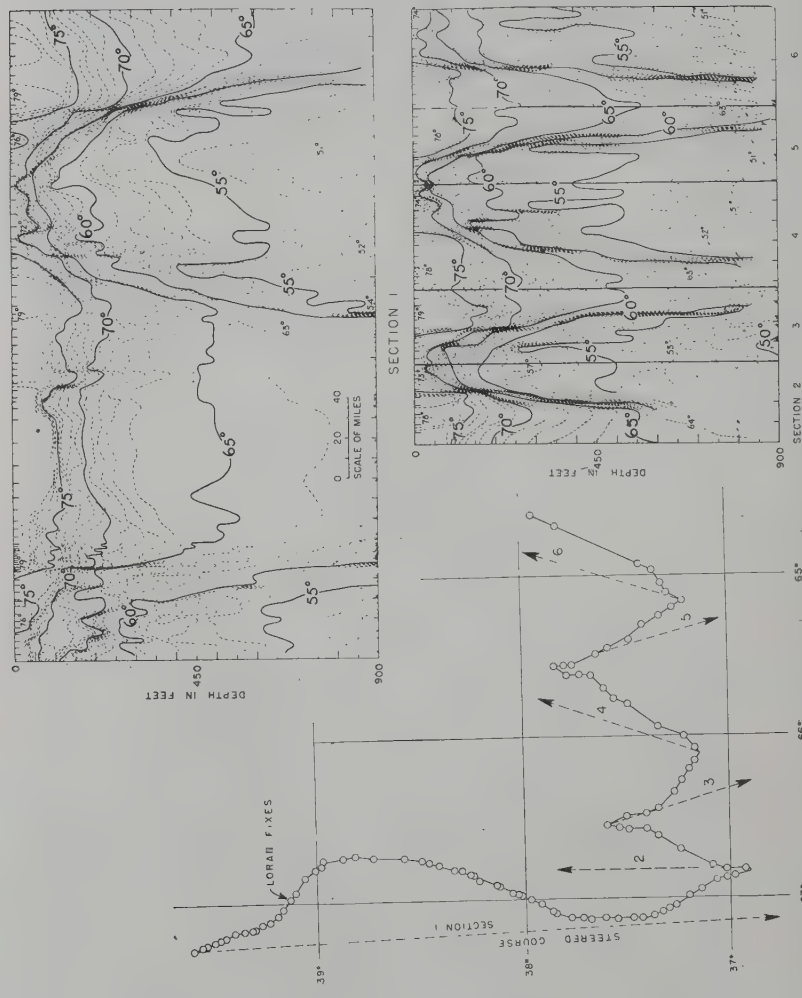


Figure 4. Currents calculated from the departure between the observed and dead reckoning positions during recent Gulf Stream surveys.


SECTION 1
SECTION 2
DEPTH IN FEET
0
450
900
SCALE OF MILES
0 20 40
LORAN FIXES
STEERED COURSE
SECTION 1
39°
38°
37°
67°
66°
65°
1
2
3
4
5
6

the usual axis of the Gulf Stream, and during this time several freighters bound for Europe were sighted. Since these ships must have been bucking this countercurrent for at least six hours, their calculated drift toward the east for a 12-hour period could not have come to more than one or two knots, even if they had spent the remainder of the time in the swiftest part of the easterly-flowing, true Gulf Stream.

EDDIES ASSOCIATED WITH THE GULF STREAM

The eddies that have been found both north and south of the Gulf Stream fall into two general classes. The *first* are frictionally-driven or shear-zone eddies, often roughly 17 miles in diameter. Spilhaus (1940) found smaller eddies of this type, which he called parasite eddies, having dimensions of the order of magnitude of four miles. The *second* are radically different from these in that they are considerably larger, rotate in the opposite direction, and are frequently found many miles away from the Gulf Stream. These eddies appear to be actual segments of the main stream that have broken away from the parent body when the Gulf Stream, in its meandering, formed an excessively large loop in its path. This would explain the existence of large cyclonic eddies south of the Stream and anticyclonic eddies north of it. The last two sections of the May 1946 cruise of the ATLANTIS (Fig. 3) showed that the Gulf Stream had then formed a large loop toward the south that could easily have been cut off later by the Stream re-forming across the northern portion. A more fully developed example was observed in June 1947 in the same area. Apparently, we are dealing with a phenomenon that is quite parallel to that observed in the regions of strong westerly winds in the upper atmosphere.

Part of the data from the June 1947 cruise is summarized in Fig. 5. The diagram illustrates the method used in all recent Gulf Stream investigations, that is, the steered course, the frequent loran fixes and the temperature-depth profiles. The relationship between the drift of the vessel (the surface current) and the temperature-depth profile is evident. Sections 2 to 6 along the southern portion of the eddy are typical of profiles crossing the swiftest part of the Gulf Stream itself. As this cruise developed, it became evident that the cyclonic eddy was over 200 miles in length, east-west, and about 60 miles wide. It was partially circumnavigated three times during a period of about eight days.

In 1945, in almost the same area, the schooner VALOR had drifted in

Figure 5. The navigational record and the corresponding bathythermograph profiles for a crossing of the Gulf Stream south of Georges Banks and also for a large cyclonic eddy (Section 1). Sections 2 to 6 extend along part of the southern edge of this eddy, the center of which was characterized by relatively cold water at all depths.

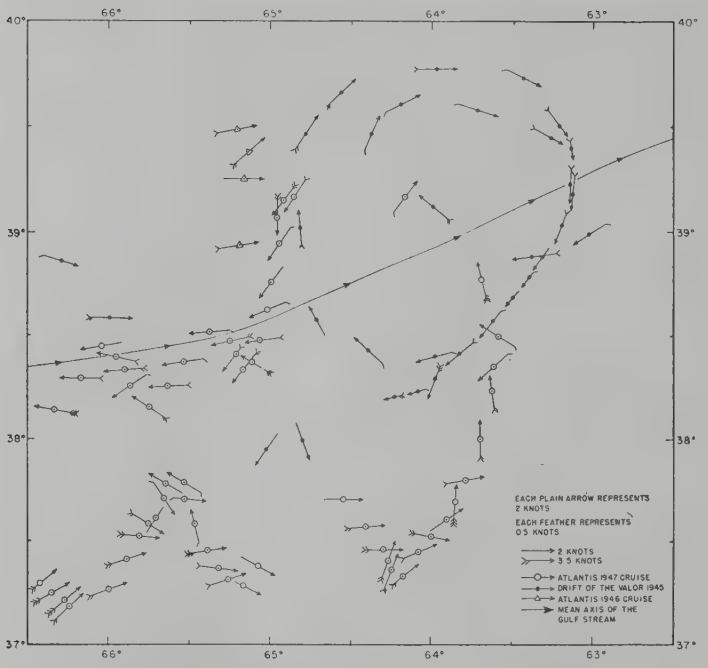


Figure 6. Comparison between the currents observed on three recent cruises and the supposed mean track of the Gulf Stream.

a powerful anticyclonic eddy for about 10 days. We are indebted to Lieut. D. T. Parson, USNR, for 48 loran fixes obtained during this period. These, plus his careful records of the drift of the vessel through the water while hove to, have enabled us to make reliable calculations of the velocities encountered. Fig. 6 combines the VALOR and ATLANTIS data. To avoid confusion, only calculated velocities of two knots or more are shown. These observations cover a considerable area through which the Gulf Stream presumably flows normally, yet only a few of the arrows point toward the east. It just happens that on all three occasions the Gulf Stream had been violently displaced; at the time of the 1945 observations it was far to the south; in 1946 the strongest current was about 50 miles north of the mean track. Admittedly, these are probably exceptional observations. The aver-

age current charts from which the normal axis of the Gulf Stream has been deduced combine many thousands of less accurate observations. Yet Fig. 6 clearly illustrates the great weakness of such charts. The average current, and the current at any one time, may be very different indeed. Strong currents flowing in deep water are subject to considerable dislocations, and moreover, these strong currents, at least in the western part of the oceans, are considerably narrower than has generally been supposed. If the Gulf Stream is typical of such currents, and it probably is, only by rapid survey techniques can we hope to gain a reasonably reliable picture of its typical behavior. Averaging data merely blurs the details which are the key to its more complete understanding.

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Contribution No. 452

SOME SEASONAL CHEMICAL CHANGES IN THE OPEN OCEAN[1]

By

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Several studies have been made of the seasonal changes in the chemical composition of sea water, especially of the so-called "nutrient substances." But most of these have been in localities relatively near shore and in the temperate zones where climatic fluctuations are relatively great. During the years 1937 and 1938 an opportunity arose to study such changes in the open ocean in connection with an investigation of the variations of the Gulf Stream (Iselin, 1940).

Three stations were chosen on a line between Montauk Point, N. Y., and Bermuda as follows: Station A, on the Continental Shelf about 30 mi. SE. of Montauk Point (Lat. 40° 40′ N; Long. 71° 45′ W); Station B, in the slope water northwest of the current of the Gulf Stream (Lat. 39° 00′ N; Long. 70° 40′ W); Station C, in the Sargasso Sea southeast of the Gulf Stream (Lat. 35° 30′ N; Long. 67° 30′ W). These stations were visited seven times during the year from October 1937 to September 1938, and determinations were made of the following chemical properties and substances: pH, alkalinity, phosphate, nitrate, nitrite, ammonia. These, along with temperature and salinity, would have afforded a comprehensive chemical picture of conditions, but, unfortunately, it was seldom possible to complete such an extensive chemical program at any one station. There are many gaps, therefore, in the chemical data, but enough information was obtained to suggest some conclusions.

The methods used were those which have been described before: pH by the indicator method using cresol red and the Hastings bicolorimeter without buffers (Mitchell and Taylor, 1935; Mitchell, *et al.*, 1936); alkalinity by the method of Mitchell and Rakestraw (1933); phosphate, nitrate, and nitrite by the standard methods of Atkins (1923), Harvey (1926), and Griess (1879) and Ilosvay (1889), respectively; ammonia by a modification of the method of Krogh (1934).

[1] Contribution No. 452 from the Woods Hole Oceanographic Institution.

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The concentration of free carbon dioxide was calculated from the pH, alkalinity, temperature, and salinity, by the procedure of Buch, *et al.* (1932).

The times at which the stations were visited were as follows:

Cruise I, October 2–9, 1937
II, December 6–16, 1937
III, January 3–5, 1938
IV, April 6–12, 1938
V, May 29–June 5, 1938
VI, July 10–17, 1938
VII, August 24–September 1, 1938

The significant results are shown in Figs. 1–6.

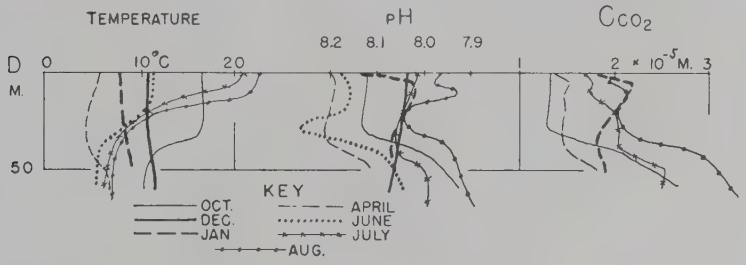

Figure 1. Temperature, pH, and free carbon dioxide concentration (C_{CO_2}) at Station A. C_{CO_2} in moles $\times 10^{-5}$.

From Figs. 1 and 2 it may be seen that the conditions at Station A were substantially the same as at other similar locations which have been studied heretofore, as, for example, the English Channel and the Gulf of Maine. During the summer months, when a strong thermocline develops, the upper levels become depleted of nutrient substances. In the winter a temperature inversion takes place, the whole water column becomes homogeneous or even unstable, and vertical circulation brings about replenishment from the richer deep water. The curves for pH and carbon dioxide concentration show vigorous biological activity going on in summer, with less in winter.

This is one of the few occasions on which ammonia and nitrite determinations have been made simultaneously, and it is important to notice that the two follow the same general pattern. Both are found at the surface during the winter and both are generally lacking there in the summer. This lends some support to the view, developed from

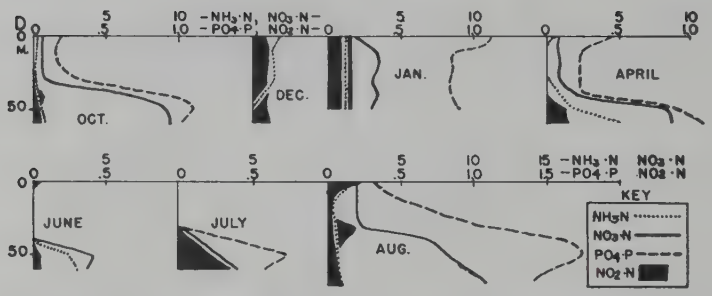

Figure 2. Seasonal distribution with depth at Station A of: ammonia-nitrogen, nitrate-nitrogen, phosphate-phosphorus, nitrite-nitrogen, in microgram atoms per liter. The upper scale of units is for ammonia and nitrate, the lower for phosphate and nitrite.

experimental studies (von Brand, *et al.*, 1937), that ammonia, which is the first product of organic decomposition, is the precursor of nitrite in the sea.

Fig. 3 shows the relation between temperature, oxygen, pH, and carbon dioxide at Station B. It will be noted that the position of the oxygen minimum follows the thermocline up and down with the seasons and, as usual, is slightly above the pH minimum. The carbon dioxide concentration, more clearly than the pH, also follows the fluctuations of the thermocline.

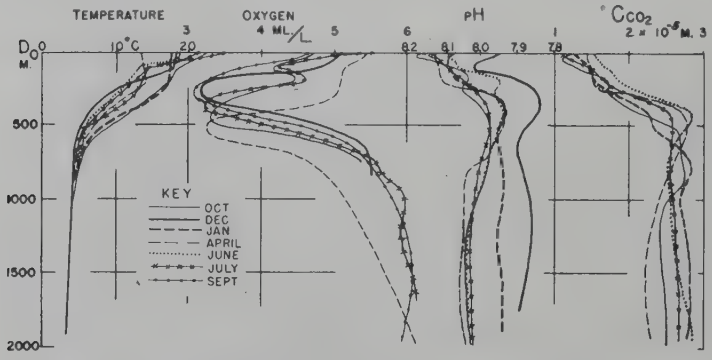

Figure 3. Temperature, oxygen, pH, and free carbon dioxide concentration at Station B Oxygen in ml/l., carbon dioxide in moles $\times 10^{-5}$.

The curves for pH at different times of the year do not coincide as closely as might be expected. There is little reason to believe that there should be as great differences at, say 1,000 meters, as are indicated. In the method for this determination, which makes use of the dissociation constant of the indicator rather than a set of standard buffers, significant errors may be introduced by using different batches of indicator, or even the same indicator over a considerable period of time. The glass electrode had not at that time been developed to its present state of reliability and convenience, otherwise the indicator could have been repeatedly standardized by this means. Consequently, although the relative values on each cruise are probably reliable, it is not safe to compare too closely the results obtained on different cruises. It would have been possible to assume that pH changes are insignificant below the thermocline and to have shifted all the curves to the right or left to make them pass through a common point at some standard depth (1,000 or 1,500 meters). The validity

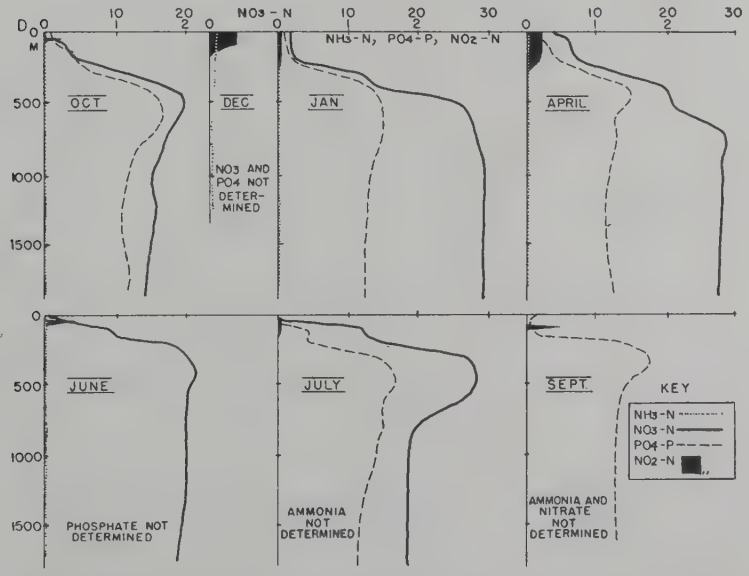

Figure 4. Seasonal distribution with depth at Station B of: ammonia-nitrogen, nitrate-nitrogen, phosphate-phosphorus, nitrite-nitrogen, in μg. at./l. The upper scale of units is for nitrate, the lower for ammonia, phosphate, and nitrite.

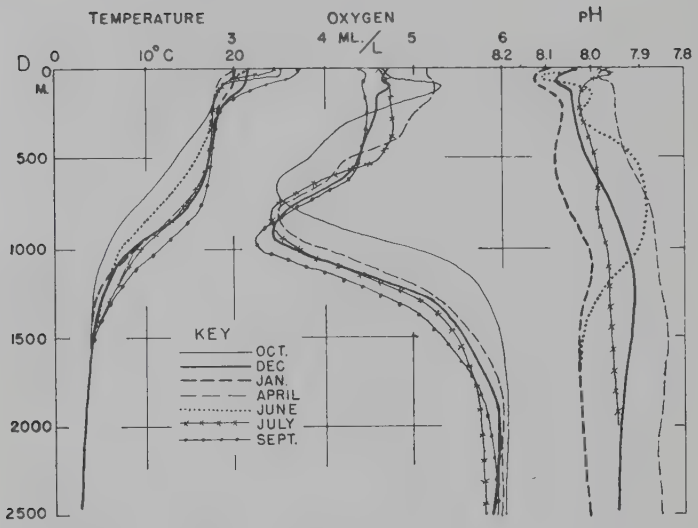

Figure 5. Temperature, oxygen, and pH at Station C. Oxygen in ml./l.

of this assumption is not certain, however, and the results of such an adjustment do not bring out any clearer relations.

The pH value is involved in the calculation of the carbon dioxide concentration, and since the variations in the latter (for five cruises) agree well with the variations in oxygen, it would seem that the pH values on at least these five cruises are fairly reliable.

Fig. 4, showing the distribution of nitrate, nitrite, ammonia, and phosphate at Station B, reveals two interesting facts. First, the positions of the phosphate and nitrate maxima fluctuate with the thermocline, which might have been expected from their close relation to the oxygen minimum. Secondly, in the upper levels, the same changes take place—although somewhat less clearly—as at Station A.

The temperature is lower at the surface in winter, and the upper layer becomes homogeneous. Vertical circulation brings nitrate and phosphate up from the transition layer to the surface. In summer, stable stratification again sets in and nutrients disappear by consumption. Nitrite also appears at the surface in winter and disappears in summer. In this case ammonia did not show as clear a relation to nitrite as at the shallower station; only in December was it found in small amounts, principally in the upper levels.

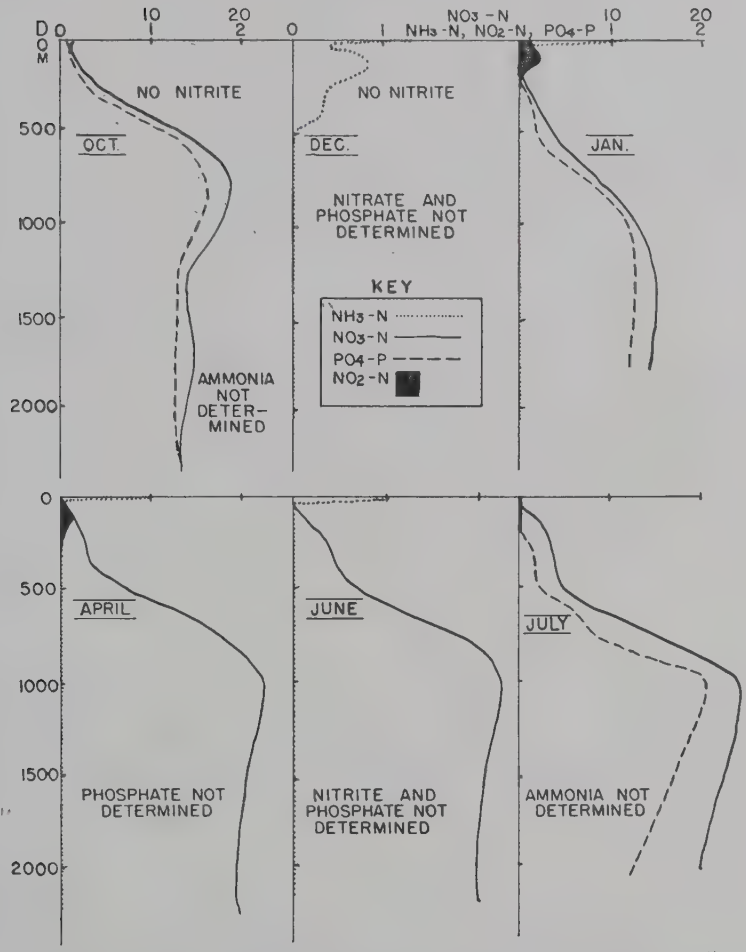

Figure 6. Seasonal distribution with depth at Station C of: ammonia-nitrogen, nitrate-nitrogen, phosphate-phosphorus, nitrite-nitrogen, in μg. at./l. The upper scale of units is for nitrate, the lower for ammonia, phosphate, and nitrite.

Nitrite appeared in the surface in December and remained through January and April; in June, July, and September, however, it had disappeared from the surface. Somewhat lower down, in a narrow

zone extending to 100 or 200 meters, significant amounts were still to be found. This is in accord with a previous study (Rakestraw, 1936).

The conditions at Station C were in general the same as those at Station B, although in some respects less clear. Fig. 5 shows the same relation between oxygen distribution and the temperature structure. The remarks already made about the pH results are equally true at this station. Although the surface values for nutrients are not conclusive, partly because of incomplete data from the December cruise, there is nevertheless a strong indication that there is not as much replenishment from the transition zone as at Station B. Thermal stratification is not completely destroyed in the winter.

For some reason, significant amounts of ammonia seem to have been present commonly in the surface, although only in December did these extend further down. Notwithstanding this, no nitrite was present at this time. This is different from the condition at Station B but it may be highly significant. It suggests that nitrite, which is never abundant in this semitropical oceanic water, had not yet been formed by oxidation of its precursor, ammonia. The ammonia, on the other hand, may have been a recent result of organic decomposition. By January, however, the oxidation had taken place, and the nitrite persisted through April until June and July, when only a small trace was found.

SUMMARY

At least to the extent to which seasonal changes in temperature, etc., take place in the upper layers in the open ocean, the seasonal variations in nutrients and other chemical factors are the same as those which occur in shallow inshore regions of the temperate zones. In addition, however, the distribution of chemical constituents and properties varies with the movements of the water mass and the changes in its physical properties, such as the rise and fall of the thermocline.

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Contribution No. 453

THE THEORY OF THE ELECTRIC FIELD INDUCED IN DEEP OCEAN CURRENTS[1]

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The Problem. Due to the fact that the water in the ocean is a conductor, and that it is everywhere under the influence of the earth's magnetic field, we should expect, by the law of electric induction, that wherever the water is in motion electric potentials and currents will be established. It is the purpose of this paper to discuss the theory of these phenomena in the deep ocean and to indicate certain analytical solutions of the problem which demonstrate the important physical aspects of electric fields associated with ocean currents.

The Fundamental Equation of the Electric Field.[2] Let $\mathbf{H}$ be the vector magnetic field intensity, ρ the scalar resistivity and $\mathbf{i}$ the electric current vector. Consider a closed curve fixed in the fluid. Let $\mathbf{v}$ be the fluid velocity vector. The length of arc along the closed curve is given by the vector $\mathbf{s}$. The element of area of the surface enclosed by the curve is $\mathbf{dS}$. Faraday's law of induction may then be expressed in the following general form,

$$\frac{d}{dt}\int\int \mathbf{H}\cdot\mathbf{dS} + \oint \mathbf{i}\cdot\mathbf{ds} = 0\ , \tag{1}$$

where the d/dt is to be understood in the manner of the substantial derivative of hydrodynamics. The first equation (1) may be transformed (Abraham and Becker, 1932: 39–40) as follows:

$$\frac{d}{dt}\int\int \mathbf{H}\cdot\mathbf{dS} = \int\int \frac{\partial \mathbf{H}}{\partial t}\cdot\mathbf{dS} + \int\int (\mathrm{div}\ \mathbf{H})\mathbf{v}\cdot\mathbf{dS} - \int\int \Big[\mathrm{curl}\ (\mathbf{v}\times\mathbf{H})\Big]\cdot\mathbf{dS}\ . \tag{2}$$

[1] Contribution No. 453 from the Woods Hole Oceanographic Institution.

[2] The author is particularly indebted to Mr. M. S. Longuet-Higgins of the Admiralty Research Laboratory at Teddington, England, for acquainting him with the basic physics involved in this section; see REFERENCES.

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In the ocean a considerable simplification of (2) is possible, because over moderately large areas $\mathbf{H}$ is constant and uniform. Therefore, the first two terms of the second member vanish, and by Stoke's Theorem the third term may be transformed to a line integral,

$$-\int\int\Big[\text{curl}\,(\mathbf{v}\times\mathbf{H})\Big]\cdot\mathbf{dS} = -\oint(\mathbf{v}\times\mathbf{H})\cdot\mathbf{ds}. \tag{3}$$

Equation (1) may now be written in the following form:

$$\oint(\mathbf{v}\times\mathbf{H} - \rho\mathbf{i})\cdot\mathbf{ds} = 0. \tag{4}$$

The vanishing of this line integral signifies the existence of the electric scalar potential function ϕ, defined in the following way:

$$\nabla\phi = \mathbf{v}\times\mathbf{H} - \rho\mathbf{i}. \tag{5}$$

The term $\rho\mathbf{i}$ involving the unknown current vector $\mathbf{i}$ may be eliminated if ρ is assumed to be uniform, for then the div $\rho\mathbf{i}$ vanishes, and upon taking the divergence of (5) one obtains

$$\boxed{\nabla^2\phi = \mathbf{H}\cdot\text{curl}\,\mathbf{v}.} \tag{6}$$

If $\mathbf{H}$ and $\mathbf{v}$ are both regarded as known, which is physically the case' then we simply have here Poisson's equation to solve for the electric potential ϕ. It is desirable to emphasize the complete generality of (6). This equation defines the electric field resulting from *any arbitrary velocity field* in the ocean.

The boundary conditions upon this equation are obtained from (5). At a nonconducting boundary the normal component of the vector $\mathbf{i}$ vanishes. If $\mathbf{n}$ is the unit vector normal to the boundary,

$$\mathbf{n}\cdot\mathbf{i} = 0,$$

so that

$$\frac{\partial\phi}{\partial\mathbf{n}} = \mathbf{n}\cdot\mathbf{v}\times\mathbf{H}.$$

At a conducting boundary, such as occurs between two media of different specific resistivity, the normal component of $\mathbf{i}$ is equal in each medium, and the potential ϕ is equal in each medium. The first condition may be expressed in terms of $\partial\phi/\partial\mathbf{n}$ for each medium by using (5).

An Idealized Particular Ocean Current System and its Associated Electric Field. The velocity and potential fields of a natural ocean

current system are very complicated functions of position. They may be treated numerically as indicated in the section, Numerical Method of Solution. An analytically simple model is advantageous, inasmuch as it shows the essential features without many complications of a purely formal but not conceptual nature. In order to exhibit some of the features of the problem, an idealized ocean current system is treated here. Rectangular co-ordinates are taken with the x,y-plane in the surface of the ocean, with the z-axis pointing vertically upwards. This ocean is supposed to be divided into two layers. The top layer, no. 1, extends from $z = 0$ to $z = -h_1$. The bottom layer, no. 2, extends from $z = -h_1$ to $z = -h_2$. The bottom of the ocean, $z = -h_2$, is taken in this discussion as nonconducting.

The velocity in layer no. 1 is supposed to be given as

$$\begin{Bmatrix} v_x \\ v_y \\ v_z \end{Bmatrix} = \begin{Bmatrix} 0 \\ v_o \cos \pi/b\, x \\ 0 \end{Bmatrix}. \tag{7}$$

Layer no. 2 is supposed to be at rest. This current system consists of alternate bands of water of breadth b moving in the positive and negative y-direction over a lower layer which does not participate in the motion. This picture is artificial, but may be generalized by implementing the Fourier Integral Theorem.

Let us suppose that the magnetic field of the earth is entirely vertical,

$$\mathbf{H} = \begin{Bmatrix} 0 \\ 0 \\ H_z \end{Bmatrix}. \tag{8}$$

Substitution of (7) into (6) gives the equations

$$\nabla^2\phi_1 = \gamma \sin \beta\, x, \tag{9}$$

$$\nabla^2\phi_2 = 0, \tag{9'}$$

where the subscript refers to the layer number, and the following abbreviated forms have been introduced:

$$\gamma = -H_z v_o\, \pi/b\,, \qquad \beta = \pi/b\,. \tag{10}$$

In order to obtain a solution of (9) and (9'), one supposes that the potential is expressible in separable form, which indeed later appears to be the case.

$$\phi_1 = \sin \beta x \cdot Z_1\,, \tag{11}$$

$$\phi_2 = \sin \beta x \cdot Z_2\,. \tag{11'}$$

Substitution of (11) and (11′) into (9) and (9′) yields, after cancelling the common factor,

$$\frac{\partial^2 Z_1}{\partial z^2} - \beta^2 Z_1 = \gamma\,, \tag{12}$$

$$\frac{\partial Z_2}{\partial z^2} - \beta^2 Z_2 = 0\,. \tag{12′}$$

The solutions of these two equations are simply,

$$Z_1 = A_1 \cosh \beta z + B_1 \sinh \beta z - \delta\,, \tag{13}$$

$$Z_2 = A_2 \cosh \beta z + B_2 \sinh \beta z\,, \tag{13′}$$

where A_1, A_2, B_1, and B_2 are constants of integration and

$$\delta = \beta^{-2} \gamma\,.$$

These constants must now be determined in terms of the boundary conditions. Take $\mathbf{n}$ as the unit vertical vector. At $z = 0$ there must be no current across the water surface:

$$\mathbf{i} \cdot \mathbf{n} = 0\,. \tag{14}$$

From (5) we have the electric current in terms of the potential

$$\mathbf{i} = \frac{1}{\rho}\left[\mathbf{v} \times \mathbf{H} - \nabla\phi\right]. \tag{15}$$

Substituting into (14) we obtain

$$\mathbf{n} \cdot \mathbf{v} \times \mathbf{H} - \frac{\partial \phi}{\partial z} = 0\,. \tag{16}$$

In the particular case we are discussing $\mathbf{n} \cdot \mathbf{v} \times \mathbf{H}$ vanishes, so that the boundary condition at the surface $z = 0$ is

$$\frac{\partial \phi}{\partial z} = 0\,. \tag{17}$$

The boundary condition at the bottom $z = -h_2$ is also one of no current, so it is the same as (17).

At the interface between layers 1 and 2, $z = -h_1$, two conditions prevail, for clearly the potential and current must be continuous. Therefore at $z = -h$,

$$\phi_1 = \phi_2\,, \tag{18}$$

$$\mathbf{i}_1 = \mathbf{i}_2\,. \tag{18′}$$

The second of these equations may be expressed in terms of the potential function

$$\frac{\partial \phi_1}{\partial z} = \frac{\partial \phi_2}{\partial z}. \tag{18''}$$

The conditions (17) at $z = 0$ and $z = -h_2$, and the conditions (18) and (18'') at $z = -h_1$, suffice to determine the constants of integration.

$$\begin{aligned} A_1 &= \delta \frac{\sinh \beta (h_2 - h_1)}{\sinh \beta h_2}, \\ B_1 &= 0 \\ A_2 &= -\delta \frac{\sinh \beta h_1}{\tanh \beta h_2}, \\ B_2 &= -\delta \sinh \beta h_1. \end{aligned} \tag{19}$$

Therefore, the final solution is

$$\phi_1 = \sin \beta x \left[1 - \frac{\sinh \beta (h_2 - h_1)}{\sinh \beta h_2} \cosh \beta z \right] \frac{v_o H_z}{\beta}, \tag{20}$$

$$\phi_2 = \sin \beta x \left[\frac{\sinh \beta h_1}{\tanh \beta h_2} \cosh \beta z + \sinh \beta h_1 \sinh \beta z \right] \frac{v_o H_z}{\beta}. \tag{20'}$$

The exact expressions (20) and (20') may be replaced by simpler expressions to a first approximation in the case where $\beta h_2 << 1$, that is, where the breadth of the current is much greater than the depth of the ocean, as most frequently happens in nature.

$$\phi_1 \cong \phi_2 \cong \sin \beta x \left[\frac{h_1}{h_2} \right] \frac{v_o H_z}{\beta}. \tag{21}$$

According to this approximate formula the lines of equipotential are vertical straight lines, and the amplitude of the potential developed is directly proportional to the ratio of current depth to ocean depth.

For shallow surface currents the return circuit beneath, in the resting water, is comparatively so large that it effectively shorts the potentials developed.

Numerical Method of Solution. A convenient numerical method of solution may be based upon the relaxation methods developed by Southwell (1946). Any vertical velocity profile can be investigated and the electric potential field computed.

Equation (6) is expressed in finite difference form. The boundary condition at the bottom and at the free surface is expressed by (16). The procedure of the solution is then by liquidation of residuals.

Publication of any of these relaxation solutions is postponed until some *simultaneous* electric potential measurements and sufficient hydrographic stations for computation of the velocity field are available.

The Effect of the Resistance of the Bottom. Longuet-Higgins and Barber (1946) have shown that the potential developed in a tidal current through a shallow channel (such as the English Channel) is greatly controlled by the resistivity of the bottom. It is important, therefore, to discover what the effect of the electric conduction through the bottom will be on the preceding analysis, which was made upon the assumption of a nonconducting bottom.

For this purpose we may introduce a layer 3 extending from $z = -h_2$ to $z = -\infty$ which will represent the bottom. The resistivity of layers 1 and 2 is ρ_1 and ρ_2, and since they are bottom sea water layers $\rho_1 = \rho_2$. The resistivity ρ_3 of the bottom is considerably greater than ρ_2. For convenience we introduce the ratio

$$\tilde{\omega} = \frac{\rho_2}{\rho_3}; \qquad 1 >> \tilde{\omega} \geq 0 .$$

The boundary conditions at $z = 0$ and $z = -h_1$ remain the same as before. For $z = -h_2$ however we now have

$$\phi_2 = \phi_3 , \tag{22}$$

$$\frac{\partial \phi_2}{\partial z} = \tilde{\omega} \frac{\partial \phi_3}{\partial z} . \tag{22'}$$

At $z = -\infty$ the potential vanishes

$$\phi_3 = 0 \text{ at } z = -\infty . \tag{23}$$

The governing equations (13) and (13′) still hold, with the addition of

$$Z_3 = A_3 \cosh \beta z + B_3 \sinh \beta z . \tag{23''}$$

The condition (23) immediately determines B_3, so that we have

$$Z_3 = A_3 (\cosh \beta z - \sinh \beta z) .$$

Again, at $z = 0$ the condition (17) shows that $B_1 = 0$.

There remain four independent constants A_1, A_2, B_2, A_3, to determine and the four boundary conditions (18), (18″), (22) and (22′). These give respectively

$$\begin{aligned}
A_1 \cosh \beta h_1 - A_2 \cosh \beta h_1 + B_2 \sinh \beta h_1 &= \delta , \\
- A_1 \sinh \beta h_1 + A_2 \sinh \beta h_1 - B_2 \cosh \beta h_1 &= 0 , \\
A_2 \cosh \beta h_2 - B_2 \sinh \beta h_2 - A_3 (\cosh \beta h_2 + \sinh \beta h_2) &= 0 , \\
- A_2 \sinh \beta h_2 + B_2 \cosh \beta h_2 + A_3 \tilde{\omega} (\sinh \beta h_2 + \cosh \beta h_2) &= 0 .
\end{aligned} \tag{24}$$

For the purpose of determining these constants it will be convenient to restrict our thoughts to the case where $\beta h_2 << 1$, that is, broad currents. The above equations are then, to a first approximation, as follows:

$$\begin{aligned} A_1 - A_2 + B_2\,\beta h_1 + 0 &= \delta\,, \\ -A_1\,\beta h_1 + A_2\,\beta h_1 - B_2 + 0 &= 0\,, \\ 0 + A_2 - B_2\,\beta h_2 - A_3\,(1 + \beta h_2) &= 0\,, \\ 0 - A_2\,\beta h_2 + B_2 + A_3\,\tilde{\omega}\,(1 + \beta h_2) &= 0\,. \end{aligned} \tag{25}$$

The values of the constants are determined to be (neglecting second and higher powers of βh_1 and βh_2)

$$\begin{aligned} A_1 &= \delta\,\frac{\tilde{\omega} + \beta\,(h_1 - h_2)}{\tilde{\omega} - \beta\,h_2} = \frac{\beta\,(h_2 - h_1) - \tilde{\omega}}{\beta\,h_2 - \tilde{\omega}} \\ A_2 &= -\,\delta\,\frac{\beta h_1}{\beta h_2 - \tilde{\omega}}\,, \\ B_2 &= -\,\delta\beta h_1, \\ A_3 &= \frac{\delta\,\beta h_1}{(1 + \beta h_2)\,(\tilde{\omega} - \beta h_2)}\,. \end{aligned} \tag{26}$$

Comparison of these values of A_1, A_2 and B_2 with those obtained for the nonconducting bottom ($\tilde{\omega} = 0$) shows that for small $\tilde{\omega}$ ($\tilde{\omega} << \frac{1}{10}$) the potential developed is affected by the presence of the bottom only negligibly. These considerations make it seem justifiable to us to ignore the resistivity of the bottom in discussion of the potential fields generated by shallow currents in the deep ocean. In the case of currents in shallow channels these conclusions do not apply.

Summary. The physical principles which describe the association of the water velocity and induced electric potential field in the deep ocean are formulated, and with the aid of a simple idealized model the chief features are discussed.

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Contribution No. 454

OCEANOGRAPHY AND GEOSYNCLINES[1]

By

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Geosynclines are one of the fundamental problems of geology. Since they are intimately related to the ocean or some inland body of marine water, knowledge of modern concepts of oceanography helps the geologist in understanding better their mode of origin. Geosynclines are masses of sediment, largely clastic in nature, 30,000 to 50,000 feet thick.[2] The deposits consist of alternating sandstone, siltstone, and shale.

The presence of sandstone, together with such features as ripple marks and crossbedding, has suggested varying conditions of deposition in shallow water. Thus the rate of settling of the sea bottom has been considered as being approximately equal to the rate of accumulation of sediment. The alternation between coarse and fine sediments has been taken as evidence of rhythmic changes in (1) sea level, (2) rate of sinking, or (3) rate of deposition, or a combination of these three factors. In the orthodox concept, sedimentation continues until the whole mass of sediment is upturned into a mountain range.

No uniformity of opinion has been reached as to how thick an accumulation of sediment is required before it is called a geosyncline, but the common figure is 30,000 feet. Although many people regard the load of sediment as instrumental in the settling of the basin, and though all are agreed that independent diastrophic forces aid the process, there is no unanimity of opinion as to the relative effects of load and diastrophism. Nevertheless many people believe that the sediments are deposited in essentially shallow water. The presence of sandstone, crossbedding, ripple marks, foreset beds, rain prints, peat, and shallow-water forms of life are evidence for this inference. However, recent work in submarine geology indicates that some if not a significant proportion of geosynclinal sediments were deposited in deep water.

Deposition of sediments in the sea is influenced materially by the physical conditions, that is, the dynamics of the water. Sverdrup, in

[1] Contribution No. 454 from the Woods Hole Oceanographic Institution.

[2] For a general study of geosynclines, see Glaessner and Teichert, 1947.

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recent years, has led the way in our understanding of the physical processes of the sea, and any geologist who is interested in learning some of these principles is referred to his works, particularly "The Oceans" (Sverdrup, *et al.*, 1942).

The principal oceanographic factors that govern deposition in geosynclines are currents, waves, wind, and configuration of the sea bottom, and to a minor extent, ecological considerations affecting the growth of organisms, including temperature and salinity of the water. To these should be added the typically geologic factors—supply of detritus and diastrophism.

Currents are of four principal types: oceanic, wind, longshore, and tidal. The oceanic currents, such as the Gulf Stream and the Japanese Current, are largely products of the open sea and are not likely to have great influence upon geosynclinal deposition, though offshoots may enter inland basins or embayments of deposition. Due to the Coriolis force, these currents in the northern hemisphere flow northward along the west side of oceans and southward along the east side. Similarly, wind-driven currents in the northern hemisphere trend in a direction to the right of the wind, and thus on the average are likely to flow northward on the west side of basins and southward on the east side, but of course such directions depend upon the direction of the prevailing wind. As both wind and oceanic currents tend to have their maximum velocities offshore, they do not materially affect deposition of sediments until the detritus has been transported some distance from the coast. Tidal currents have their greatest influence in lagoons and estuaries. In some bodies such as the Gulf of Mexico they have little effect.

Longshore currents on the other hand have a pronounced effect upon geosynclinal deposition. As Sverdrup and his co-workers (Putnam, *et al.*, in press) have shown, longshore currents commonly are formed by waves that approach the shore at an angle, with their course along the beach in the general direction with which the waves approach the beach. Since the waves are formed by the wind, the prevailing wind has a decided effect upon the transport of detritus along the shore. The proportion of fine particles in the detritus influences materially the type of deposition. If the proportion of fine material is large, currents may transport the bulk of the sediment a long distance from the mouth of the streams before it is deposited. If it is small, most of the sediment is likely to be laid down near the mouths of the streams, unless the longshore currents are strong.

Currents may extend with varying velocity to the bottom of the sea. Irregularities on the sea floor interfere with the free movement of the currents and may set up eddies which interfere with deposition.

Consequently, sediments over humps or ridges on the sea floor, or even along slopes that are relatively steeper than adjacent parts of the sea bottom, are likely to be coarser than deposits in adjoining areas. In as much as the effect of shape of the sea bottom is independent of depth of water, coarse sediments may be found in water of any depth.

Waves influence deposition by stirring up the bottom in shallow water, thus effecting a winnowing action, which tends to cause sediments on flat continental shelves to be relatively coarse, even at considerable distance from shore and in water up to 100 fathoms in depth. Waves also wear back the coast lines and thus supply detritus. Their effect upon the profile of equilibrium of the sea floor is not yet well understood, but it may take a very long time for the so-called profile of equilibrium to be reached, during which interval of time sea level may change, thus causing the ocean to seek a new level of equilibrium.

In recent years oceanographers have found that internal waves, which never reach the surface, are more common than was formerly thought. Active research is in progress, which may indicate that internal waves are capable of generating currents that affect the transport and winnowing of sediments at considerable distances from shore and in great depths of water.

The wind, as mentioned above, profoundly affects the waves, and in turn the currents. It also influences the climate and ecologic conditions of sedimentation.

The configuration of the basin of deposition probably has a greater effect on geosynclinal deposition than has been generally recognized in the past, because of its pronounced influence on currents, both along shore and in deep water.

The relationship of ecology to geosynclinal deposition is too complicated to discuss here, but the temperature of the water may have a profound effect. For example, if the water is very cold, settling velocities of detritus are lessened, with the result that sediment will be transported greater distances before it is deposited. Similarly, the mixing of fresh and salt water at river mouths has decided effects upon coagulation and settling of clay particles.

With respect to supply of detritus, pertinent factors are: rate of supply, grain size, strength and constancy of the currents, and configuration of the basin adjacent to the rivers that supply the debris. Even though a river carries a heavy load, if all the particles are fine-grained, currents may remove the detritus almost as fast as it arrives. The mode of origin of bars and beaches is understood by geologists, but the formation of submerged bars or underwater dunes is less well understood. The latter have been observed in several places in recent

years, even at some distance from shore, and they may be more common than has been recognized.

Much is spoken about foreset beds upon deltas. The formation of foreset beds depends upon the development of an essentially flat but gently sloping surface of deposition terminated by a more abrupt slope, down which detrital particles can roll after they have been pushed off the topset part of the delta. The angle of inclination of the foreset beds depends to some extent upon the depth of water at the forward edge of the topset beds. In glacial lakes or fjords, where the water level may have risen very rapidly with respect to rate of delta formation, the detritus may be dumped into relatively deep water, with the result that the classic type of steep foreset beds may form. But in the sea where the rate of change in level of the water in general is much slower than in glacial lakes, the depth of water at the front of the topset beds may be relatively shallow, with the result that the angle of inclination of the foreset beds may be comparatively small, perhaps only one or two degrees. Consequently steep foreset beds are not likely to be characteristic of marine deltas, except of course in lagoons and sloughs along delta distributaries.

Diastrophism, as has been pointed out by many geologists, has a dominant influence on geosynclinal deposition. It affects the supply of detritus by governing the gradient of streams and by influencing wind, temperature and rainfall. It affects the deposition of debris by changing the configuration of the sea floor. Fluctuations in rate of diastrophism may lead to rhythmic alternations of sediments.

Much of what has been said above is familiar to most geologists, but perhaps certain aspects have not been emphasized in the past as much as they deserve. Among such aspects are: (1) The relationship between supply of detritus and longshore currents, (2) the effect of wind upon sedimentation, (3) the relationship of configuration of the basin to deposition, (4) the existence of relatively strong currents in deep water, which lead to deposition of coarse sediments far from shore, (5) the lack of steep foreset beds on large deltas and, (6) material differences in rate of settling with respect to rate of deposition.

In order for sediments to accumulate in shallow water, these two rates must be essentially the same. If they are the same, either the influx of debris fortuitously balances the rate of sinking or the influx of debris controls the rate of settling. Natland (1933) has shown that the succession of foraminifera in the present Channel Islands region of California from deep water to shallow water is essentially the same as in the Lower Pliocene formations in the near-by Los Angeles basin. This relationship suggests that the lower beds in the Lower Pliocene were deposited in deep water and that the basin filled up with relatively

little additional sinking. A similar sequence of foraminifera has been reported from the Lower Pliocene in the Eel River basin in California. Thus it would seem that, at first, downwarping was greater than rate of sedimentation, following which sedimentation was greater than settling. As Barrell (1913, 1914) has pointed out for the Devonian geosyncline in Pennsylvania, the basin eventually filled up and continental beds were deposited, thus pushing the shoreline seaward. Hence deposition was more rapid than settlement.

Recent work by Trask, Phleger and Stetson (1947) in the Gulf of Mexico has confirmed this concept. In the central part of the Gulf, in water more than 11,000 feet deep, foraminiferal ooze is underlain at depths of 2 to 10 feet by alternating clay, silt, and sand containing a distinctly cold water fauna, characteristic of the waning stages of the Ice Age. The sand and silt is extremely well-sorted. In two places crossbedding or ripple marks were found in coarse clastics of the Ice Age deposits; in two other places, well-sorted sand zones, one and three feet thick respectively, were encountered at depths of more than three feet beneath the surface of the sediments. Such deposits, if hardened into rock and found in a geosyncline, would be taken as compatible with the idea of shallow-water deposition. Yet they were encountered in 11,000 feet of water.

If these sediments are of shallow-water origin, then within the last 20,000 to 100,000 years either the water of the Gulf of Mexico has been lowered more than 10,000 feet, or the sea bottom has been depressed that amount. Either idea is contrary to prevalent concepts. Of course, the continental glaciers might have been much thicker than they have previously been considered, with the result that 10,000 feet of water might have been removed from the sea. Such an idea is in accord with the subaerial origin of the many submarine canyons that have now been found. The low level might have prevailed for only a few thousand years, since most submarine canyons do not have deep or wide gorges. Such a concept, however, is contrary to prevailing opinion.

Similarly, if the sea floor has been lowered, the rate of settling would be one foot in 2 to 10 years—truly a rapid rate. Also, if the sea floor settled 10,000 feet, where did the mass of rock beneath the floor of the Gulf go? No corresponding recent rise of sea level in adjacent lands has been observed, unless one wishes to ascribe some of the uplift of the Mexican Plateau to recent downwarping of the Gulf. Such an idea of course is most unorthodox.

The concept of deposition in shallow water thus seeming to be anomalous, the only alternative is deposition of the sediments in deep water. If the well-sorted sand, three feet thick, was deposited in

11,000 feet of water, as were also the crossbedded sands and the numerous well-sorted silt layers, then the water must have been in motion to account for the high degree of winnowing exhibited by the sediments. Perhaps internal waves caused such motion. At any rate, the presence of such phenomena, ordinarily ascribed to shallow water, is most peculiar. Geologists might do well to exercise caution when ascribing a shallow-water origin to sediments upon such evidence as well-sorted sandstone, crossbedding, or ripple marks.

SUMMARY

In conclusion, the data presented in this paper support the inference that deposition in a geosyncline is a function of the ratio of rate of deposition to the rate of settling. If the rate of settling is greater, the sediments may accumulate in deep water; if the rate of deposition is greater, particularly in the later stages of the formation of the geosyncline, the sediments may accumulate in shallow water or upon land. Mathematically, the sequence of events may be expressed by the following equation:

$$ds/dt - dd/dt = f(D),$$

where ds/dt is the rate of settling, dd/dt is the rate of deposition, and $f(D)$ is a composite function representing the combined effects of diastrophism throughout the areas of loading and unloading of the sediments, together with the effect of diastrophism upon climate.

Perhaps such a mathematical formula is of little meaning at present, but ultimately, as geology, like every other science, becomes more quantitative, tangible values can be substituted in the equation. When that day comes geologists will be able to interpret with satisfaction the mode of origin of the geosynclines they study.

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Contribution No. 455

Reprinted from THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA, Vol. 20, No. 4, 498–503, July, 1948
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Reflection of Underwater Sound from the Sea Surface*

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Contribution Number 455 from the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts
(Received February 19, 1948)

Information on the instantaneous sea surface reflectivity for 30-kc sound has been obtained. The method required that the submerged source and receiver be rigidly mounted on towers resting on the sea bottom. Transmission of a frequency-modulated sound pulse results in an interference pattern at the receiver; interference occurs between the direct and reflected sound. Analysis of these interference patterns reveals the following: The average time of persistence of the pattern is five-hundredths of a second. Under the conditions of the experiment, surface reflectivity is highly frequency dependent. The median value for the reflection coefficient is near to unity. Approximately 10 percent of the time the sea surface focuses the sound, giving a a reflection coefficient greater than unity.

I. INTRODUCTION

THE sea surface has always been regarded as an important factor in the propagation of sound in the sea. Because practical sound sources and receivers lack perfect directionality, surface reflected sound can rarely be excluded in underwater reception. The intensity of the reflection undoubtedly depends in part on the sea surface topography. However, the surface topography, in general, is highly irregular and does not easily lend itself to an exact mathematical treatment of sound reflection. Additional complications arise because the sea surface is constantly changing. Consequently, there exists only a limited amount of theory to serve as a guide to our knowledge of reflection from actual sea surfaces.[1,2]

The present work is primarily concerned with the direct measurement of the reflection of the sea surface. The method was specifically developed for making instantaneous reflection measurements *in situ*. The measurements were performed in Buzzards Bay in the vicinity of Cape Cod.

The following sections give, in turn, the elementary theory of interference from a plane sea surface, the experimental technique of making measurements in the sea, and the reflectivity properties of a rough sea surface which are obtained from the data.

II. THEORY OF INTERFERENCE FROM A PLANE SURFACE

It is highly informative to begin by assuming a perfectly plane sea surface. Suppose that a directional sound source and receiver are located below the sea surface. The received sound will travel by two paths: directly from source to receiver, or by reflection from the surface. The two rays will interfere at the receiver and will reinforce or cancel, depending upon the phase difference. Let

d = amplitude of the direct ray at the receiver,
r = amplitude of the reflected ray at the receiver,
θ = phase angle between the direct and reflected rays at the receiver,
a = resultant amplitude of sound reaching the receiver,
f = sound frequency,
λ = sound wave-length, "
Δ = path difference (ft.) between direct and reflected rays, and
V = velocity of sound (ft./sec.).

The customary formula for the summation of two waves of identical frequency is

$$a^2 = d^2 + r^2 - 2dr \cos 2\pi(\Delta f / V). \qquad (1)$$

The minus sign takes into account the reversal in phase on reflection.

In these experiments the geometry is fixed, with the frequency variable. Consequently, the

* This work represents one of the results of research carried out under contract with the Bureau of Ships, Navy Department.
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[1] L. S. Ornstein, Physica 4, 1181 (1947).
[2] Carl Eckart, University of California, Division of War Research, Report No. M407, March 20 (1946).

maximum resultant amplitude $(d+r)$ will occur when

$$f=(2n-1)(V/2\Delta),\ n \text{ an integer.}$$

The minimum amplitude, $(d-r)$, occurs when

$$f=n(V/\Delta),\ n \text{ an integer.}$$

These two equations illustrate the method on which the measurements are based. The frequency is varied and maxima and minima are received at the hydrophone. Measurements of the amplitude of the maxima and minima can be used to calculate the reflection coefficient using the relationship:

$$\text{reflection coefficient}=\frac{r}{d}=\frac{\text{max.}-\text{min.}}{\text{max.}+\text{min.}}. \quad (2)$$

In order to make an "instantaneous" observation of the reflection coefficient by this method it is necessary to observe the interference pattern in a short time; the frequency must be shifted

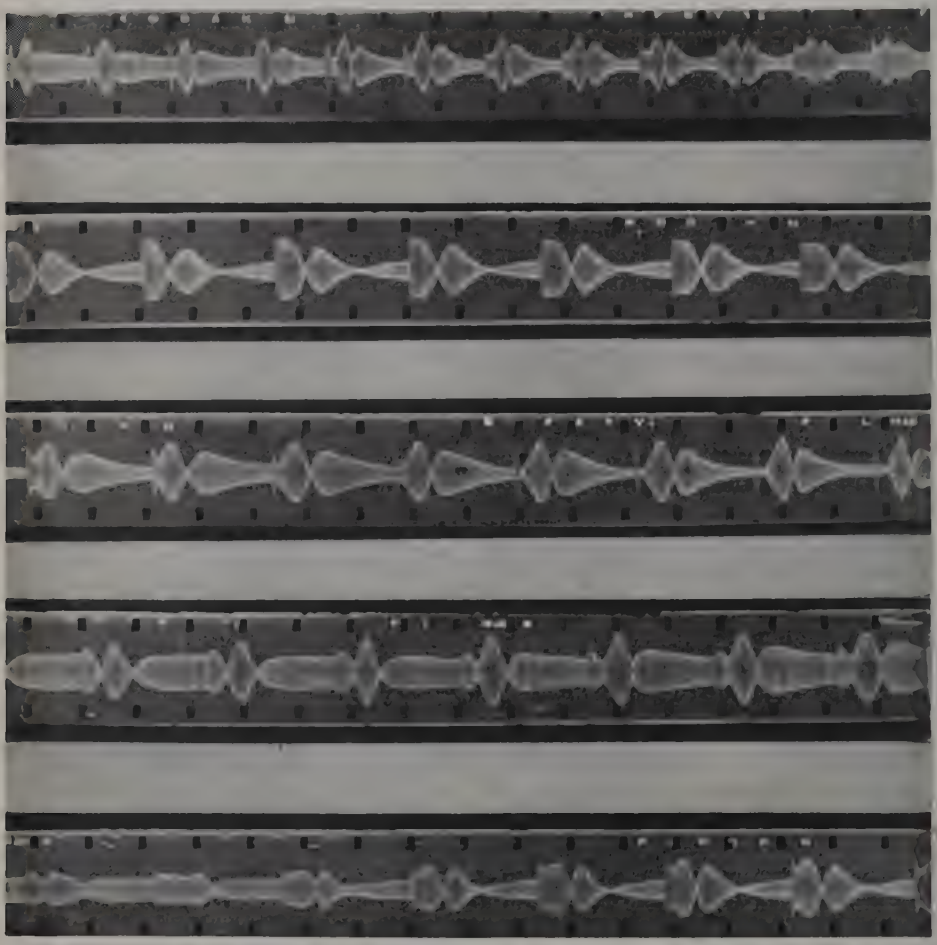

FIG. 1. Sample oscillograms showing interference between the direct and reflected rays. The initial part of each interference pattern is marked by a sharp spike, the frequency increased to its highest value in one fiftieth of a second and then instantaneously returned to the initial frequency. The cycle was repeated giving a succession of interference patterns each being formed in one-fiftieth of a second.

TABLE I. Amplitudes of maxima and minima for 30 consecutive pulses.

Sweep number	First maximum	Minimum	Second maximum
1	45	24	36
2	45	19	40
3	44	16	45
4	46	14	47
5	47	14	44
6	48	14	49
7	51	12	49
8	52	9	49
9	53	5	48
10	55	3	49
11	56	3	51
12	57	4	51
13	59	6	54
14	59	9	54
15	61	9	56
16	60	10	59
17	61	10	59
18	60	9	59
19	60	10	59
20	59	9	60
21	57	5	60
22	57	5	60
23	57	7	60
24	55	7	61
25	54	6	62
26	53	4	61
27	52	5	62
28	49	4	59
29	46	7	58
30	43	10	54

with great rapidity. Because of the finite travel time difference along the two paths, there will exist a slight difference in frequency between the reflected and direct waves at the receiver. Although Eq. (1) assumes the two waves to have identical frequencies, it will be shown that the perturbation of the interference pattern is slight. It is usual to describe the instantaneous sound pressure, when the frequency is not constant, by the function

$$\sin 2\pi\phi(t).$$

The instantaneous frequency $f(t)$ is then

$$f(t)=d\phi/dt,$$

or

$$\phi(t)=\int_0^t f(t)dt.$$

Hence the instantaneous sound pressure is proportional to

$$\sin 2\pi\int_0^t f(t)dt.$$

If t_0 be the travel time for the direct ray, and $(t_0+\Delta/V)$ the travel time for the reflected ray, the resultant amplitude at the receiver is

$$a=d\sin 2\pi\int_0^{t_0} f(t)dt-r\sin 2\pi\int_0^{t_0-(\Delta/V)} f(t)dt,$$

the minus sign again being introduced by the change in phase on reflection. A second-order approximation in (Δ/V) is

$$a^2=d^2+r^2-2dr\cos 2\pi \times\{(\Delta/V)f(t)+\tfrac{1}{2}(\Delta/V)^2f'(t)\}, \quad (3)$$

where $f'(t)$ is the time derivative of the instantaneous frequency. This equation differs from Eq. (1) only in the term $\frac{1}{2}(\Delta/V)^2f'(t)$. Throughout these experiments, $f(t)$ changed from 27 kc to 33 kc at a rate no greater than 300,000 cycles per second per second. In this case, $\frac{1}{2}(\Delta/V)^2$ is negligibly small and can be neglected. Thus, the simple interference pattern predicted by Eq. (1) is not significantly altered.

III. EXPERIMENTAL PROCEDURE

Experimental procedure consisted, in brief, of transmitting a rapid series of frequency modulated pulses to a receiver. The received pulses were recorded and the interference pattern of each pulse analyzed to obtain the reflection coefficient.

In order to avoid introduction of errors resulting from the pitch and roll of a ship, the projector and receiver were mounted on steel towers which rested on the ocean bottom. The towers were located about 150 feet apart in 44 feet of water; a transducer was fixed to each about 10 feet below the surface at mean tide. Thus the grazing angle of the sound was approximately 8 degrees.

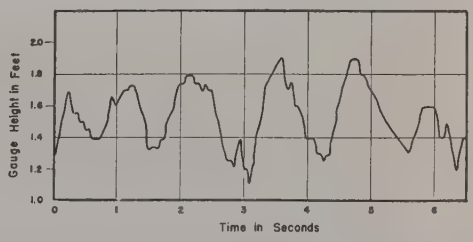

FIG. 2. Portion of wave height record for one day.

The two transducers were identical, being constructed of 8-inch diameter mosaics of rochelle salt crystals. These transducers had a response which was independent of frequency over the useful range. In view of its importance to the interpretation of the results, this fact was carefully checked by fastening source and receiver on a rigid mount approximately 2 feet apart. When the mount was lowered far beneath the sea surface, frequency sweep oscillograms taken with the arrangement outlined below showed no detectable amplitude change. Both transducers were connected by means of 300-foot cables to the electrical apparatus on the ship.

The frequency-modulated signal generator consisted of a triode in series with a condenser, the two being connected across the resonant circuit of an oscillator. When a saw-tooth voltage was applied to the grid of the triode, the oscillator frequency was shifted accordingly. The output oscillator was fed to an inverse feed-back amplifier which in turn was connected to the sound source. The frequency range was 27 to 33 kc; the sweep rate usually 50 per second. The simple frequency modulation circuit described above could not be expected to give a linear change in frequency with time over a relatively large frequency range. The effect of this nonlinearity is to make the separation of the adjacent maxima and minima in the recorded interference pattern non-uniform; this has no effect on the determination of the reflection coefficient.

The received signal was amplified and connected to the vertical plates of a cathode-ray oscillograph. The vertical deflection on the oscillograph screen was photographed with a motion picture camera whose intermittent drive had been replaced by a uniform film motion.

Sample oscillograms taken with the arrangement outlined above are given in Fig. 1. The initial part of each frequency sweep is marked by a sharp transient; the frequency increased to its highest value in one-fiftieth second and then instantaneously returned to the initial frequency and the cycle was again repeated. Table I is a representative sample of the data giving the measured maxima and minima amplitude for 30 successive interference patterns covering an elapsed time of 0.6 second.

Data on the topography of the sea surface

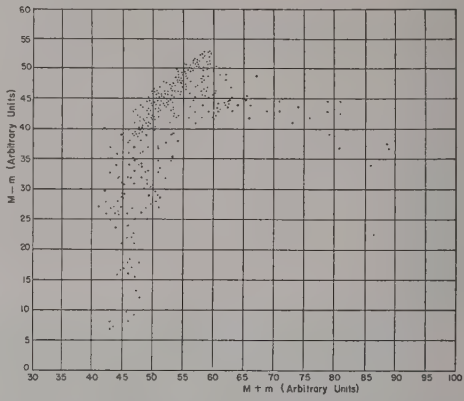

FIG. 3. Plot of $(M-m)$ *versus* $(M+m)$ for one day. The significance of the diagram is made clearer if one assumes the sea surface is plane. In this case $M+m=2d$; $M-m=2r$. However, if $r>d$ (reflection coefficient greater than unity) then $M+m=2r$ and $M-m=2d$. Hence all the points should lie either on a vertical or horizontal line, depending on whether the reflection coefficient is less or greater than unity.

were obtained with a 6-foot scale which was fastened to the tower with part of the scale immersed in the water. The intersection of the sea surface and the scale was photographed with a motion picture camera at 16 frames per second. A sample plot of the instantaneous wave height *versus* time is given in Fig. 2. These records yielded information on the average wave height, the wave motion, and the depth of the transducers during the experiment.

IV. TIME AND FREQUENCY DEPENDENCE OF SEA SURFACE REFLECTION

Two facts can be obtained by preliminary inspection of the data: First, successive interference patterns are approximately reproduced; the time rate of change of the interference pattern is slow compared to the sweep time of one-fiftieth of a second. This means that the reflectivity properties of the sea, under these particular conditions, persisted longer than 0.02 second. An autocorrelation analysis of these data gives the average persistence of the reflectivity of the order of 0.05 second. Possibly the time of persistence is some function of the surface topography. These measurements were made with sea conditions which were somewhat varied. The median wave height on the calmest day was

TABLE II. Distribution of reflection coefficients.

Date (1946)	Median wave height in feet	Amplitude of direct ray	Reflection coefficient			
			Lower decile	Median	Upper decile	Highest
6/28	0.2	24	0.21	0.67	1.12	1.29
7/3	0.3	25	0.20	0.72	1.12	1.48
7/8	0.8	23	0.22	0.65	1.35	1.65
7/9	0.4	28	0.32	0.75	1.05	1.28
7/10	0.4	22	0.50	1.04	1.46	2.00
7/11	0.6	20	0.25	0.95	1.80	2.20
7/16	0.6	22	0.36	0.96	1.82	2.10
7/17	0.7	22	0.23	0.77	1.50	1.91

0.3 foot; the roughest day had a wave height of 0.8 foot. There are no significant changes of the persistence time of the patterns within these limited varieties of surface conditions.

Although successive interference patterns approximately reproduce, successive maxima within the same pattern do not. Lack of reproduction of successive maxima signifies that the amplitude of the reflection is dependent on the sound frequency. This is not unexpected. The reflecting surface is not smooth, so the reflected sound is not a single ray but the result of many rays. The reflected amplitude can be represented in the form

$$r=\sum_{1}^{n} r_n \cos 2\pi f[t-(\Delta_n/V)].$$

The phase angle, $2\pi f(\Delta_n/V)$, clearly is frequency dependent; the summation, r, is also frequency dependent. In addition, the individual amplitudes, r_n, may possibly be slightly frequency dependent, but this effect is undoubtedly smaller.

V. REFLECTION COEFFICIENTS OF THE SEA SURFACE

Analysis of the amplitudes of the maxima and minima in the pattern brings out other results. These can best be studied with the aid of a diagram which is illustrated in Fig. 3. Here the sum of the amplitudes of adjacent interference maxima and minima, $(M+m)$, is plotted *versus* the difference of the same extrema, $(M-m)$. All of the interference patterns obtained for one day are plotted in this way on the diagram.

The significance of the diagram can best be understood by neglecting the frequency dependence of the reflection. In this case, according to Eq. (1), the maxima and minima will have the value $(d+r)$ and the absolute value of $(d-r)$, respectively. Hence the abscissa for each point, $(M+m)$, will have the value $2d$; the ordinate $(M-m)$, will be $2r$. However, when reflection occurs in which the reflected amplitude is *larger* than the direct amplitude, the significance of $(M-m)$ and $(M+m)$ is interchanged; the sum is now $2r$ and the difference $2d$. To summarize, all points for which $r<d$ will approximately lie on a vertical line whose abscissa is $2d$; the points for which $r>d$ will lie on a horizontal line whose ordinate is $2d$.

The diagram shows that this simplified picture is approximately correct. The amplitude of the direct sound d is approximately constant, having the value 23. The appreciable scatter of the points is due to the fact that the values of M and m used for plotting a single point occurred at frequencies separated by approximately 2000 cycles. The reflected sound r is variable, its most probable value lying between 20 and 25. Surprisingly, the reflected sound was often greater than the direct sound, occasionally being greater by the factor two.

An instantaneous reflection greater than the direct sound occurred on all days at least 10 percent of the time. From these results it must be concluded that the sea surface often focuses the sound at the receiver, causing the reflected amplitude to be greater than the direct. There are two mechanisms by which such focusing could occur. One possibility is that the portion of the surface illuminated by the sound occasionally takes the shape of a concave mirror with source and receiver fortuitously at conjugate foci. The second possibility, more likely than the first, is that the sound is reflected from many separated distinct areas on the surface analogous to the highlights produced by the reflection of sunlight from the sea surface. Occasionally separate reflections arrive at the receiver nearly in phase and increase the amplitude. In the former possibility, the reflection will not have appreciable frequency dependence; in the latter case, the sound will definitely be frequently dependent for the reason discussed previously. The data showed the focusing effect to be strongly frequency dependent.

It might be expected that the median wave height may be correlated with the sound reflec-

tion properties. It has already been stated that the median wave height had no appreciable influence on the persistence time of the reflectivity. Table II gives the median reflection coefficient[3] defined by Eq. (2) for each median wave height. In addition, the upper and lower deciles are listed. As can be seen from the table, no correlation exists between the rather limited distribution of wave heights and the median reflection coefficient. Possibly the wave height has some influence on the spread of the reflection coefficient; the spread seems to diminish for calmer seas.

The author acknowledges the valuable aid of Mr. Arthur Yaspan, who assisted with the analysis of the data and with the preparation of the manuscript.

[3] The values for the median reflection coefficient given in the table are essentially in agreement with those of Urick and Saxton, J. Acous. Soc. Am. 19, 8 (1947).

Contribution No. 456

Reprinted from JOURNAL OF METEOROLOGY, Vol. 5, No. 5, October, 1948, pp. 238–240
Printed in U. S. A.

NOTE ON EDDY DIFFUSION IN THE SEA

By Lewis F. Richardson
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(Manuscript received 28 April 1948)

We have observed the relative motion of two floating pieces of parsnip, and have repeated the observation for many such pairs at different initial separations. The interest of this simple experiment lies in its relation to the extensive historical background of fact and theory. Some of the background, though published, is not as yet well known, so that a brief review of it seems desirable.

When eddy diffusion was first noticed by Taylor [10] and by Schmidt [9], they naturally supposed that its quantitative relations were like those of molecular diffusion. Fick's equation

$$\frac{\partial v}{\partial t} = K \frac{\partial^2 v}{\partial x^2}, \tag{1}$$

in which t is time, x is distance along a straight line, v is the concentration of the diffusing substance, and K is a constant called the diffusivity, had been known for half a century as a description of the diffusion of salt in still water.

Taylor, Schmidt, and their successors, applied this equation to an atmosphere which had been smoothed by averaging its condition at any point over a time such as an hour. This type of smoothing leaves conspicuous vertical gradients, from which, with other data, K was deduced. The results have been most valuable. It was found indeed that K was not constant, but varied with height. So a fresh start had to be made from an amended form of Fick's equation in which K was a function of x. This complicated the integrals, but involved no fundamental change of ideas.

In contrast with this success there was an astonishing misfit when Fick's equation was applied to the diffusion of a cluster of smoke. For this purpose x was sometimes a horizontal coordinate. The smoke is usually densest in the middle. The size of the cluster is suitably measured by the standard-deviation σ of the smoke particles from a mean plane. It is then a logical consequence of Fick's equation that

$$d\sigma^2/dt = 2K. \tag{2}$$

This relation was apparently first published by Einstein [3] in a theory of Brownian motion. It asserts that $d\sigma^2/dt$ is independent of σ. But in the atmosphere

[1] Contribution No. 456.

$d\sigma^2/dt$ was found to increase enormously with σ. Thus Defant [1, 2] found K to be of the order of 10^{11} cm^2 sec^{-1} when cyclones are treated as eddies in the mean circulation of their latitude. Richardson and Proctor [5] and Richardson [6] showed that Defant's $K = 10^{11}$ cm^2 sec^{-1} is not isolated, but is the climax of a continuous variation from the molecular diffusivity $K = 0.2$ cm^2 sec^{-1}. It is a commonplace in physics that so-called constants may vary somewhat with circumstances. In particular any measure of atmospheric diffusion is likely to depend on the roughness of the earth's surface, and on the vertical gradients of temperature and of mean wind. Nevertheless the variation of K in a ratio of a billion is too large to be excused by 'circumstances.' The variation of K depends on a geometrical quantity σ, and Fick's equation is also geometrical in so far as it contains $\partial^2/\partial x^2$. For this reason it is difficult to regard the variation of K as an outer circumstance detached from Fick's equation. There appears to be a fault in the equation itself. Richardson [7] tried to improve Fick's equation by introducing terms

$$\sum_r \sum_s K_{rs} \frac{\partial^{r+s} \nu}{\partial x^r \partial t^s}.$$

These however did not lead to agreement with observation.

Another problem was raised by the contrast between the success of Fick's equation as applied to vertical gradients, and its failure as applied to clusters observed mostly in projection onto the horizontal plane. An explanation put forward by Richardson and Gaunt [8] is as follows. Every form of diffusion is a compensation for some preliminary smoothing. The form of the law of diffusion is likely to depend on the type of preliminary smoothing. Experience shows that when the smoothing is by averages taken over long times then Fick's law, in which K may be a function of position, is appropriate. When however the smoothing is by averages taken over a smoke-cloud which is dispersing and so becoming larger, then Fick's law is quite unsuitable. Horizontal diffusion may differ somewhat from vertical diffusion; but that is not the main cause of the contrast between the respective failure and success of Fick's equation; it is the different manners of smoothing that are the main cause.

The present experiments relate to a theory [6] in which the fundamental concepts are remarkably different from those of Fick. Instead of the position x we have the projected separation l of a pair of marked particles. It should be explained that l is the projection of the separation onto any fixed direction. Instead of the concentrations ν we have q, the number of neighbors per unit of l. The transformation from $\nu(x)$ to $q(l)$ is

$$q(l) = \int_{-\infty}^{\infty} \nu(x)\nu(x + l)dx. \tag{3}$$

If it is independently known that the cluster is symmetrical in the sense that $\nu(x) = \nu(-x)$, then the reverse transformation, starting from a given $q(l)$, leads to a unique $\nu(x)$. This can be proved by a slight modification of a theorem published by Kendall [4], and attributed by him to Wiener [11]. Instead of the diffusivity K we have $F(l)$ the "diffusivity for neighbours." Instead of Fick's equation (1) we have

$$\frac{\partial q}{\partial t} = \frac{\partial}{\partial l}\left(F(l) \frac{\partial q}{\partial l} \right). \tag{4}$$

In a hypothetical fluid, diffusing in accordance with Fick's law, it has been proved [6] that $F(l)$ would equal $2K$. In the actual atmosphere the diffusion of clusters is such that to mention K at all is rather confusing. However, this confusion has often been made, and it can be remedied approximately by setting

$$F(\sigma) = 3.03K, \tag{5}$$

where, as before, σ is the standard deviation of the cluster. To obtain $F(l)$ thus, via a self-contradictory K, from measurements of σ which involves a great variety of separations, is an inaccurate and untidy procedure. A far better method for measuring $F(l)$ is to observe particles in pairs. Some preliminary experiments should be made in order to select a suitable short time T during which l will vary measurably, and yet by only a small fraction of itself. Let l_0 be the initial value of l, and l_1, its value T seconds later. Let observation be repeated for many pairs of particles, each pair having the same l_0 and drifting during the same T. Then ideally

$$F(l_0) = \frac{\text{mean of } (l_1 - l_0)^2 \text{ for all pairs}}{2T}. \tag{6}$$

This looks like a mistake, because the standard deviation of two particles l apart is $\sigma = \frac{1}{2}l$; so that $\sigma_1^2 - \sigma_0^2 = \frac{1}{4}(l_1^2 - l_0^2)$. Nevertheless the theory [7] leads to $(l_1 - l_0)^2$ as stated in equation (6).

In practice the initial l_0 may be imperfectly equal, and $l_1 - l_0$ may not be as small as the theory requires. If so, $F(l_0)$ in equation (6) should be replaced by F of the mean of $\frac{1}{2}(l_0 + l_1)$ taken over all pairs. For the atmosphere the first estimate of $F(l)$ was made via equation (5) and gave $F(l) = 0.6\, l^{4/3}$ cm^2 sec^{-1} for the wide range

$$10^2 \text{ cm} < l < 10^6 \text{ cm}. \tag{7}$$

Later observations via equation (6) are published in [7]. They are in rough agreement with previous estimates. The height, localities, and weathers were all miscellaneous; so that it is not surprising to find some scatter in $F(l)$. Any power between $l^{1.3}$ and $l^{1.5}$ would be a tolerable fit to the observations.

The facts and theories relating to $F(l)$ in the atmosphere have now been reviewed.

TABLE 1. Pairs observed at Blairmore Pier.

l_0 (cm)	l_1 (cm)	l_0 (cm)	l_1 (cm)
49	94	260	14
218	95	33	59
30	31	272	204
135	71	33	11
50	26	213	134
167	275	7	7
11	18	235	223
139	58	23	18
52	61	200	179
117	76	62	31
14	39	236	272
155	93	5	15
6	15	168	213
188	179	66	101
25	33	134	93
289	418	0	17
25	33	164	53
320	317	34	53
27	27	196	159
187	188	26	0
6	15	223	227
138	126	6	5
45	14		

As far as we know, the only observations so far published on $F(l)$ in water are a few made roughly in a river [8]. They gave

$$F(l) = 2.2 l^{1.0} \text{ cm}^2 \text{ sec}^{-1}$$
$$\text{in the range } 10 \text{ cm} \leq l \leq 45 \text{ cm}. \quad (8)$$

In the sea we used floats of parsnip because it is easily visible, and because it is almost completely immersed so as not to catch the wind which, moreover, was slight. The floats were about 2 cm in diameter. An optical device was used for measuring the distance l in a fixed azimuth. The observations were made in latitude 56°0′N, longitude 4°54′W from Blairmore Pier, Loch Long, Scotland, on 6 January 1948, where the sea water was about two meters deep. In order to eliminate any change in $F(l)$ with time, we observed alternately with large and small l_0, as may be seen from table 1. From equation (6) the function $F(l)$ was computed separately for the wide and close pairs:

	wide pairs	close pairs	unit
l	187.7	26.7	cm
$F(l)$	84.3	6.4	$\text{cm}^2 \text{ sec}^{-1}$

The power law which fits these data is

$$F(l) = 0.07 l^{1.4}. \quad (9)$$

It is most interesting to find approximately the same power, $l^{1.4}$, coming out of observations made both in the atmosphere and in the sea, in circumstances such that Fick's law would lead one to expect $l^{0.0}$.

We are conscious of various imperfections in the sea-water experiment: T, 30 seconds, was rather too long; the range of l_0 was very short compared with that in the atmosphere; and the wooden posts of Blairmore Pier may perhaps have affected the result. These posts were of square section 30 × 30 cm and were arranged in two rows 410 cm apart and nearly parallel to l. The distance between centers in the row was about 270 cm. A suspension bridge would have been an ideal platform.

Although there were these imperfections, we think that the experiment raises the question whether it is a general characteristic of fluids in large volumes that $F(l)$ should vary as $l^{1.4}$.

(*Note added in proof.*—After this manuscript was submitted the writers have read two unpublished manuscripts by C. L. von Weisaecker and W. Heisenberg in which the problem of turbulence for large Reynolds number is treated deductively with the result that they arrive at the 4/3 law. The agreement between von Weisaecker and Heisenberg's deduction and our quite independent induction is a confirmation of both.)

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Contribution No. 462

WOODS HOLE OCEANOGRAPHIC INSTITUTION

Contribution No. 462

REPORT ON INVESTIGATIONS OF THE PROPAGATION OF THE SOFT-SHELL CLAM, MYA ARENARIA

Prepared in accordance with Contract,
Effective July 1, 1948, for the
DIVISION OF MARINE FISHERIES
DEPARTMENT OF CONSERVATION
COMMONWEALTH OF MASSACHUSETTS

DECEMBER 31, 1948

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PREFACE

The following report, prepared by Harry J. Turner, Jr., is a summary of the investigations of clam propagation undertaken by the Woods Hole Oceanographic Institution in 1947 and continued after July 1, 1948 under contract with the Division of Marine Fisheries, Massachusetts Department of Conservation.

Through the Committee of Clam Technicians of the Atlantic States Marine Fisheries Commission contact has been maintained with other investigators in the field of shellfish research. Three appendices included in this report were submitted in preliminary form to this Committee.

Appendix I entitled "A Report of the Soft-Shell Clam Industry on the East Coast of the United States" contains a summary of the biology of the soft clam and a review of the present status of the clam industry. Appendices II and III deal with preliminary observations on clam predators. Appendix IV entitled "The Soft-Shell Clam Fishery of Massachusetts" was written by Mr. Charles L. Wheeler, now Assistant Biologist for the Division of Marine Fisheries. Its purpose is to show how varied are the conditions of the industry in different parts of the coast and how these influence the attitudes and methods of management in the several towns.

The investigations were carried out under the leadership of Harry J. Turner, Jr., Biologist of the Woods Hole Oceanographic Institution. Those participating were John C. Ayers and Charles L. Wheeler, biologists, Helen Landau, research assistant, James Gast and Emerson Hibbard, summer assistants, and Marcus H. Howes, consultant.

Alfred C. Redfield
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Woods Hole, Massachusetts
December 31, 1948

Report on Investigations of the Propagation of the Soft-Shell Clam, Mya Arenaria

BY

Harry J. Turner, Jr.

SUMMARY

The investigations have lead to the following conclusions:

1) Setting of the soft clam may be induced on barren areas by resurfacing the flats with materials which are available in many of the salt marsh banks along the coast.

2) Seed clams as large as 1¾ inches in length may be successfully planted by broadcasting on untreated flats.

3) Predators, particularly horseshoe crabs and blue crabs may be so destructive to soft clams that transplantation and other efforts to increase clam abundance may be ineffective unless adequate methods of control are practiced.

INTRODUCTION

For the past eight years, production of the soft clam in Massachusetts has been declining steadily. This has been due in part to the condemnation of progressively larger areas because of pollution. In addition, many of the intertidal flats which were formerly considered good clamming areas have produced fewer and fewer clams. As a result a large part of the product which was formerly obtained locally has had to be imported from Maine and Canada.

A summary of what is known about the biology of the soft clam and factors which affect its distribution, growth, and abundance is given in Appendix I.

The investigations to be described were undertaken in 1947 to add to this knowledge and particularly to determine what factors affect the abundance of soft clams so that improvement programs might be put on a sound basis.

The following reasons for the general scarcity of soft clams were given by Mr. Earnest W. Barnes, Biologist for the Division of Marine Fisheries in 1947 in his report to the Legislative Commission established for the purpose of studying the shellfish situation.

1. Failure of normal sets to appear in all areas except grossly polluted ones.

2. Mortality, after a short interval of normal growth, of most all the scattered seed which did show up.

3. Failure of shellfish to fill out.

4. An unusual abundance of shellfish enemies.

In view of these conclusions it seemed expedient to make intensive investigations to determine underlying causes, and if possible develop methods by which clam abundance could be increased. Barnstable Harbor was selected because it was a clam producing locality within easy access of the laboratory where intelligent shellfish officers made full use of State Shellfish Aid programs and had maintained a progressive replanting program for some years. In addition it had formerly been the location of a successful private clam farm, and there was considerable interest among many of the inhabitants in developing some of the barren areas for this purpose with private capital.

It was decided that the following phases of the clam problem offered the greatest promise of results.

1. Investigation of the factors which affect setting and growth of the soft clam with the aim of developing methods of causing spat to collect on barren flats so that repopulation might take place naturally.

2. Study of methods of transplantation to determine how stocks of clams in polluted areas might be utilized more effectively to repopulate barren flats.

3. Study of growth, mortality, and the effect of predators to determine their effect on clam production so that methods of recognizing and overcoming adverse factors might be developed.

An investigation was also conducted on the hydrography of Barnstable Harbor. The purpose of this was to establish the rate of exchange of the waters within the harbor with those of Cape Cod Bay. This information would be useful in determining whether clam larvae which were spawned within the harbor would be likely to remain there during their free-swimming period. Information was also obtained on the effect of temperature on the spawning period and the relationships of the chemical constituents of the harbor water to the production of clam food.

The Woods Hole Oceanographic Institution secured a shallow draft 20 foot power boat, renamed the "David L. Belding", and an 8′ by 16′ scow especially for the investigation and supplied other equipment including microscopes, water samplers, plankton nets and other standard oceanographic apparatus. A small building was rented near the boat basin in Barnstable Harbor for the storage of tools and apparatus.

METHODS OF INDUCING THE SET

Scientific knowledge of factors which affect setting of the soft clam is exceedingly meager. See Appendix I. However there have been a few observations of intense sets occurring on flats which were newly created as a result of dredging operations in the Annisquam River, Yarmouthport channel, and Plymouth harbor. In addition Marcus Howes, a resident of Barnstable who operated a private grant from 1911 to 1926 attributed much of his success to sets induced by resurfacing barren flats with materials taken from a nearby marsh bank.

Seven acres of barren flats were made available by the Selectmen of Barnstable and a number of preliminary experiments were conducted to determine what soils might be suitable for spat collecting. Six small plots were resurfaced with from five to ten tons each of soils taken from marsh banks and bottom of one of the channels. Two of the experimental plots received soils identical with those which had been used by Marcus Howes in his former operations. Mr. Howes was employed as a consultant and demonstrated exactly what soils he had used.

The physical nature of the soils used in these experiments varied considerably. The material dredged from the bottom of the channel was a sticky soft mud. Other materials taken from the marsh banks contained peat with fine sand interspersed among the organic fibers. The material recommended by Mr. Howes consisted of clods of marsh grass roots and fine sand which was taken from a particular thatch island after stripping off the top layer of living sod. Top sod was also used on one of the plots.

The preliminary resurfacing experiments were completed in early August 1947, and by the end of that month small clams began to appear on all the resurfaced areas. Occasional seed could be found on the untreated control areas but the occurrence was rare and the numbers far less than in the experimental areas. Setting continued throughout the early fall.

During the winter, severe storms and ice flows carried away the transplanted soils from all the plots except those which had been resurfaced according to Mr. Howes' directions. When the latter plots were sampled in the early spring of 1948 they were found to contain clams in densities averaging 25 per square foot. The scattered seed which had appeared in some of the control areas had completely disappeared.

With these encouraging results it was decided to set up an experiment on a scale which more nearly approached practical proportions. A plot 100 feet square was staked out and resurfaced with materials taken from the same bank as were those which had survived the previous winter. This required 75 tons of material and the operations were not completed until the first week in July.

Small clams began to appear in this plot in early August and by the end of that month a good set had occurred. Sample diggings made at the end of August showed that the area was well populated with densities as great as 312

per square foot in some places. The specific importance of the clods in holding the set was indicated by the fact that small clams could seldom be found in soft sand which had been washed in between the clods along the edge of the experimental area. See Figure 1. It was also observed that the fibrous consistency of the new material afforded considerable protection to the newly set clams by preventing enemies such as crabs and drills from digging in.

An attempt was made to determine the properties which made this material suitable for spat collecting. Sieve analyses were made of the barren flats, existing clam beds, and the resurfacing material. It was found that sand from

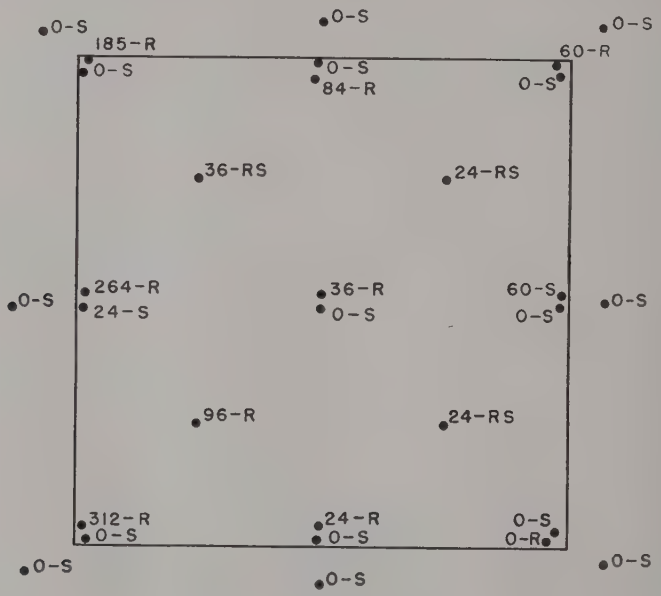

Figure 1. Distribution of seed clams in and around resurfaced area. R—clods of root masses, S—loose sand, RS—roots in loose sand.

the barren flats was deficient in the finer grain sizes when compared with sediments taken from existing clam beds. The new material included a high proportion of very fine sand grains as well as a considerable amount of root fiber.

These observations suggest that the large sand grains on the barren flats when set in motion by water currents and wave action either crush the larvae or cause them to seek another locality, while those setting on more compact areas containing finer sediments or root fibers are able to attach and dig in.

METHODS OF TRANSPLANTATION

For a number of years transplantation of soft clams from polluted to clean areas has been practiced in Massachusetts. Since over half the clam producing areas of the state are contaminated by domestic and industrial sewage, this practice provides a means by which shellfish stocks which would be otherwise unusable may be eventually made available for human consumption. However this replanting program has not been carried out to the fullest possible extent largely because of the cost.

In addition to the expense of the initial digging, replanting has been accomplished by the time-consuming and costly method of plowing in. This method involves plowing a furrow with a hand plow, scattering seed clams in the furrow, and plowing a second furrow turning the soil over the first to bury the seed. The second furrow is then seeded and the operation continued.

Replantings in general have been quite successful in some localities but there have been occasions when they were a total loss. Sometimes entire stocks have disappeared for unknown reasons, and reluctance to invest heavily in replanting has grown up in towns where such misfortunes have occurred.

Investigations made early in the century have shown that the soft clam possesses considerable burrowing ability and there are reports of successful replantings accomplished by simply broadcasting the seed on the open flat as the tide advances. Conversations with shellfish officers who have had considerable experience in transplantation revealed that there was some doubt as to whether seed clams could bury themselves sufficiently in some of the harder flats unless some sort of pretreatment was given to loosen the surface.

A study of the burrowing activities of clams of various sizes was made with the aid of a time lapse motion picture and it was found that small clams could readily bury themselves in from ten to fifteen minutes with the greatest activities exhibited by clams of the smaller sizes.

As a field test, 40 bushels of seed were obtained from the Boston Harbor area and replanting was effected by a number of methods. These included plowing in, broadcasting on the untreated flat, and broadcasting after the surface had been loosened to various depths with a rake or plow. The experiment was enlarged by the activities of a number of grant holders who planted a total of 583 bushels by a number of methods including those described above.

When the planted areas were observed on a succeeding low tide it was found that practically all the seed had dug in, the exceptions being a few clams in excess of 1¾ inches in length which made up an insignificant proportion of the total. Flats which had been planted by the plowing-in method presented a cleaner appearance because broken and dead clams were buried along with the viable stock, but no real advantage in this method could be determined. In fact it appeared that better distribution could be obtained by the broadcast method, and no pretreatment could be established as being necessary. Observations conducted during the winter and early spring showed that survival was good in all areas and it was concluded that the time-consuming and expensive plowing-in method could be profitably abandoned.

THE EFFECT OF PREDATORS

Crabs and crab-like organisms, boring snails, drills, and shore birds have been shown to feed on soft clams, but there are no precise records in the scientific literature which determine exactly how much these enemies limit clam abundance. The menace of predators has been thought to be sufficient to warrant considerable expenditures by both the coastal towns and the Commonwealth in an attempt to control them by employing men to police certain flats at low tide.

The transplanting experiments previously described provided an excellent opportunity to determine how serious the predator problem can be. The transplanted stocks which had gone through the winter of 1947-48 in relatively undiminished numbers began to decline rapidly in the late spring of 1948. This decline continued into the early summer so that by the first week in August the beds were entirely depleted.

During this period large numbers of horseshoe crabs appeared and exhibited such intensive burrowing activity that the surface sands on the planted beds thus loosened were carried away by water currents and the level of the beds was considerably depressed. The ability of the horseshoe crab to dig out and eat soft clams was checked in the laboratory. The results are detailed in Appendix II. It was determined that one horseshoe crab could eat all the clams in one square foot of a moderately well seeded flat each day.

One of the plantings of the town of Barnstable was investigated to determine how effective the conventional predator control measures might be. It was found that horseshoe crabs caused a loss of nearly 40% of the planted clams in two seasons in spite of the dilligent efforts of two deputy shellfish officers, who made daily collections. Destruction by the boring snail, another pest which is considered serious, was much smaller, as it accounted for only 3% of the clams originally planted.

An excellent opportunity occurred to determine the destruction by two other predators, the blue crab and the fiddler crab. These organisms need only be considered along the coast of the southern part of the state since Cape Cod forms the northern boundary of their range. In the Little River area of South Dartmouth, a grantholder, Mr. Morgan H. Plummer, observed that blue and fiddler crabs were causing considerable destruction to an intense set which had appeared in late May 1948. He protected several small areas by laying strips of ¼-inch galvanized screen over the flats. By the middle of the summer all the seed in the surrounding area had disappeared but the clams under the screen continued to survive. When the screens were removed in November he found the density of the seed to be 175 per square foot. This demonstrated conclusively that the predations of the blue and fiddler crabs may be one of the chief causes for scarcity of clams in the areas where they occur. See Appendix III for details.

DISCUSSION

The most significant information which has come out of the investigations to date is the determination of the magnitude of predator destruction of the soft clam. It is suggested that efforts be concentrated toward devising more effective methods to replace those currently employed to control predators which have been shown to be only partially effective. In continuing the present investigation, a program of testing such methods as trapping and fencing is being contemplated. It is the opinion of the investigators that any other form of shellfish improvement is unlikely to succeed as long as the predator population maintains a high level.

If adequate methods of predator control are devised, it has been shown that other methods of increasing the abundance of soft clams have considerable promise. Methods of inducing sets by resurfacing, although still in preliminary stages of testing may prove to be sufficiently effective to justify development of many of the barren flats of the Commonwealth under public or private management. Methods of soil analyses are being considered with the aim of devising simple tests by which the suitability of materials for developing barren areas could be quickly and easily determined.

It has also been shown that transplantation of seed taken from polluted areas could be materially increased by employing the broadcast method of replanting. It is suggested that simple machinery could be devised which could be so designed as to distribute clam seed evenly and rapidly.

APPENDIX I

THE SOFT-SHELL CLAM INDUSTRY OF THE EAST COAST OF THE UNITED STATES*

BY

HARRY J. TURNER, JR.

The purpose of this report is to bring together as much information as is available about the soft-shell clam and the clam industry so that the Committee of Clam Technicians may have a concrete basis for discussion of problems affecting that industry. Present knowledge of the biology of the clam, summarized in the first section, is based on literature cited in the bibliography at the end of the report. Production and price statistics were furnished by the United States Fish and Wildlife Service. These data are supplemented by additional information obtained from the conservation departments of the coastal states extending from Maine through New Jersey.

Economic aspects of the clam industry are discussed at the production level only. The basic problems of the clam resources could best be attacked at this level. Investigation into the economics of processing and distribution of clams are beyond the scope of this report.

Contact was made with authorities from each of the coastal states either in person or by mail. Valuable information on geographical problems was secured in this manner. It was also possible to gain a considerable insight on different attitudes toward the clam industry as they prevail in different sections of the coast. Further information on shellfish improvement programs of several Massachusetts towns was obtained by Mr. Charles Wheeler who interviewed local officials and studied their statements in town reports.

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*This report was presented in preliminary form to the Committee of Clam Technicians sponsored by the Atlantic States Marine Fisheries Commission, May 17, 1948. The author gratefully acknowledges the helpful comments and suggestions provided by the members of the Committee. Appreciation is expressed to Dr. J. Carl Medcof of the Atlantic Biological Station, St. Andrews, N.B. for his cooperation in making available data derived from his experimental program sponsored by the Dominion of Canada. Part of the expenses incurred in collecting the data and compilation of this report was borne by the State of Maine Department of Sea and Shore Fisheries.

BIOLOGY OF THE CLAM

RANGE

The soft clam, *Mya arenaria*, occurs on the east coast of North America from the Arctic Ocean south to Cape Hatteras. It is found in abundance as far south as New Jersey but occurs in such small numbers from New Jersey to Cape Hatteras that no significant industry has been developed there.

The bulk of the clam crop comes from the intertidal zone. In some localities clams are secured by special methods in water as deep as five feet at low tide, and small quantities occasionally are taken by dredge fishermen as an incidental part of the catch. Verrill gives the seaward range as being from the half-tide mark to 40 fathoms. All specimens he took in deep water were young. The upper limit with respect to tide has not been determined with certainty.

The greater part of the commercial clam crop is produced north of Cape Cod where a tide range of eight feet and more exposes extensive flats at low water and facilitates digging. South of Cape Cod there is less exposed area at low water due to a smaller range of tide and shellfish must often be dug under water. Here the fishermen find it more profitable to limit their underwater digging activities to the hard clam which lives nearer the surface of the bottom and may be harvested with rakes and tongs.

LIFE HISTORY

Spawning. The sexes are separate. Spawning occurs during the late spring, summer, and early fall. A two-and-one-half inch female spawns approximately three million eggs, and a male of that size produces sperm which number in the billions. Males and females extrude their sex products into the water where the motile sperm swim toward and unite with the eggs. The fertilized egg develops in a few hours into a larva which can swim.

Temperature is believed to determine the season of breeding. In New Jersey the first spawning occurs in May. As one passes northward along the coast, the spawning begins progressively later in the year. The duration of the breeding season is not exactly known, but there is evidence that it may extend well into the fall. Sets of clams are often found in the early spring which are so small that they can have had little time to grow before winter set in.

The stimulus which sets off the act of spawning has not been determined. Mature clams which contain ripe eggs or sperm may be induced to spawn experimentally by placing them in water a few degrees warmer than that to which they have been accustomed. More extensive work on the mussel has shown that the presence of reproductive products of the opposite sex acts as a stimulus to spawning. If this is also true of the clam, it is evident that in well populated beds the spawning of a single individual may set off a burst of spawning among

the others. This will insure a high percentage of fertilization since large numbers of eggs and sperm will be in the water at the same time.

The Free Swimming Period. As soon as the larva has developed swimming organs, it swims freely in the water feeding on suspended material. This probably consists of bacteria and small animal and plant cells. Its powers of locomotion are not great enough to much more than keep it afloat. Dispersal occurs as a result of water currents. While swimming about in the water, the larva passes through a series of developmental stages.

The duration of the free swimming period depends on the temperature of the water. Warmer waters favor more rapid development so that the larval period may be as short as twelve days in Massachusetts while in Maine it may be extended to three weeks.

Setting. By the end of the free swimming period the larva has acquired most of the organs characteristic of the adult. It is still too small to be distinguished with the unaided eye and under the microscope looks somewhat like a small quahaug. At this stage the swimming organ begins to degenerate and the larva settles to the bottom where it crawls about with its foot. It then attaches to some object by means of a thread or byssus similar to that found in the adult mussel. It may attach to sand grains, seaweed, rocks, thatch-grass, or other objects. The power at attachment remains until the young clam has grown to a length of ¼ inch.

After attachment the young clam feeds and grows. At first growth is more rapid in the anterior-posterior direction so that by the time the clam can be seen by the naked eye it has the general shape of the adult. It may detach at any time and crawl short distances in search of a more favorable locality. Finally if it comes to rest on a bottom with favorable characteristics, the young clam burrows in and attaches itself to sand grains in the sides of the burrow. If washed out it will burrow in again, and if conditions are not suitable, it may dig its way out and migrate short distances by crawling with its foot. As a rule, the young clam is permanently established in its burrow before it is an inch long. It retains its power to dig for some time in the event that scouring frees it from its burrow. However this ability becomes less with increasing size so that clams over 2 inches long seldom bury themselves when exposed.

The effect of the type of soil on setting and growth is not well understood. It has been demonstrated that the soil acts mainly as a support since food is supplied from the water above. The physical nature of the soil has been shown to have some influence on clam production. Loose shifting soils do not catch sets and often kill adults by filling the siphons with sand. Firm mixtures of sand and mud or soils compacted and cemented by algal growth appear to be the best.

The chemical nature of the soil is believed to be of little significance, although recent studies have indicated that there may be unknown substances in certain soils which cause mortality. In general, however, it is considered that the only unfavorable soils are those which cause decalcification of the shell by acid substances resulting from the decomposition of organic matter.

The soft clam lives in water containing 8 to 28 parts of salt per thousand. Thus clams occur in harbors and estuaries where sea water may be diluted with as much as three times its volume of fresh water. The distribution of the better clam beds indicates that setting and growth may actually be favored by waters containing somewhat less salt than is found in normal sea water.

Feeding and Growth. The food of the adult clam consists of material floating in the water. For some time it was believed to consist mainly of living microscopic plants such as diatoms and other algae, but recent studies of related species indicate that organic detritus may form the bulk of the food of molluscs. Organic detritus is a term given to material consisting of the dead bodies of small plants and animals, clumps of bacteria, and decomposing fragments of larger organisms.

The rate of growth of the young clam is influenced by a variety of conditions including temperature, time of submergence, availability of food, current, degree of crowding, and probably several others. To a certain degree warm water favors rapid growth but excessively high temperatures are detrimental. Clams which live near the low tide level grow faster than those at higher levels because they have more time to feed during each tidal cycle. A strong current serves both to bring in new supplies of food and also to remove detrimental waste products. Under crowded conditions competition for food as well as accumulation of waste products may seriously inhibit growth.

Spawning Age. From Massachusetts south where growth is rapid, most clams probably spawn when one year old. There are some indications that clams which set in the early summer in these localities may spawn in the fall of the same year but the number of eggs produced by them is probably small. Nothing is known concerning the spawning age of clams in the regions north of Massachusetts.

As the adult clam continues to grow the yearly production of eggs or sperm becomes greater. However in clams of great age the reproductive organs degenerate and result in the familiar "waterbellies" which are useless for propagation and low in meat yield. The life span of the clam is estimated to be about ten to twelve years in Massachusetts and may be longer in the northern localities where growth is slower.

PRODUCTION AND GROWTH

The rate of growth of the clam has been recorded for Rhode Island, Massachusetts, and New Brunswick. Graph Figure 2 shows average rates in these localities.

The difference in the growth rate has been shown to depend on the temperature. Investigations made in Massachusetts have determined that clams stop feeding when the temperature drops below 37°F, thus restricting the growing season to the warmer months of the year. In the more northern regions where winters are longer the growing season is reduced accordingly.

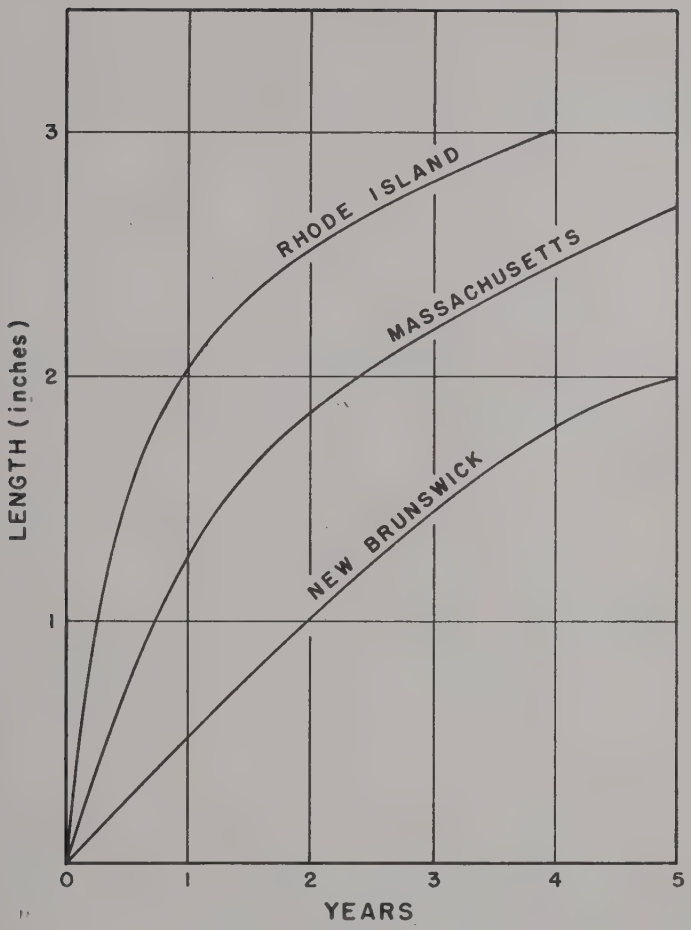

Figure 2. Growth rates of the soft-shell clam for Rhode Island, Massachusetts, and New Brunswick.

Commercial clams, which are generally at least two inches long, may be produced in one year in Rhode Island, two to two and one-half in Massachusetts, and four and one-half to five years in New Brunswick. One acre of land populated with 25 two-inch clams to the square foot will contain 540 bushels. The wet weight of the meats which may be shucked from this quantity equals

8100 pounds or a little over four tons. Some particularly favorable localities sometimes support as many as 50 clams per square foot and double the production. As the length of clams is increased, their volume and weight go up in an exponential manner. The following table shows the product of one acre containing 25 clams per square foot at different lengths.

Length	Bushels per acre	Pounds of Meat per acre	Age R. I.	Age Mass.	Age N. B.
2 in.	540	8100	1	2-2 1/2	4 1/2-5
2 1/4 "	735	11025	1 1/3	3	6
2 1/2 "	1063	15945	2	3 1/2	7
2 3/4 "	1356	20340	2 1/2	4 1/2	

ENEMIES AND DISEASES

Predators. In the free swimming stage clam larvae are probably attacked by all kinds of animals which feed on plankton. Considering the numbers of eggs that are spawned each season, the mortality at this stage must be very great. As soon as setting has occurred three groups of bottom-living animals may further reduce their numbers. These enemies are crabs and crab-like organisms, boring snails, and starfish.

The lady crab and the blue crab dislodge young clams by agitating the sand and eat them after crushing the shells with their claws. Their destructive influence is limited to small clams in soft sand. Greater destruction is caused by the horseshoe crab which burrows through the flats devouring young clams in large numbers. See Appendix II.

Among the boring snails, the oyster drill may cause considerable destruction to small clams after they have set. The drill bores a hole through the shell with its rasp-like tongue and sucks out the contents. Greater destruction is caused by the cockle *Polynices* which can burrow down a considerable distance into the soil and attack clams of a larger size. This snail operates in essentially the same manner as the oyster drill but its larger size and burrowing ability makes it a serious pest. It is estimated that a two-inch cockle can destroy 26 clams per month.

The starfish, which is one of the most serious pests to the oyster industry, has only a limited destructive influence on clams. It operates by attaching the sucker-like appendages on its arms to both shells of the clam and exerting a steady outward pull until the shells open. It then protrudes its stomach and digests the contents. Small starfish sometimes eat small clams which have not yet burrowed but the destruction of larger clams is limited to those washed out of the sand by scouring. Other predators include shore birds and bottom feeding fish but their importance has not been determined.

The clam-worm, *Nereis*, which is often found in large numbers in clam beds, has been thought by some to prey upon live clams. However, careful studies have shown that this worm is a scavenger and does not harm live clams. Its presence in the shells of dead clams is due to its habit of feeding on the bodies of clams which have died from other causes. Ecological studies have

shown that clam worms are often found in association with clams and it is possible that their presence in certain soils indicates environmental conditions favorable for clam growth.

A tubeworm, *Clymenella*, is sometimes found in flats where conditions do not favor clam growth. This worm does not directly affect the clams but indicates that the conditions are unfavorable and must be changed in some manner before the beds may be made productive.

Methods of control. Some communities which carry on planting operations employ men to police the beds and pick up cockles and crabs. Aside from this no methods of controlling predators have been developed.

Competitors. The soft clam sometimes occurs in localities where conditions are favorable for other species as well. Clam beds located where conditions favor the growth of the blue mussel are often overgrown by this species. When this occurs the beds become carpeted with mussels and as a result setting of clams is discouraged and growth is inhibited.

The thatch-grass, *Spartina*, is believed to overgrow clam producing areas when sedimentation has built the beds up to a point high enough above low tide so that the grass can survive. However, the growth of thatch islands usually results in marginal extensions of the flats as a result of sedimentation. Clumps of thatch-grass may be beneficial in acting as natural spat collectors, and it is often observed that the best digging occurs around such clumps.

Diseases. From time to time whole populations of clams die out simultaneously leaving the individuals rotting in their shells. Nothing is known as to what causes this. It has been suggested that pollution spreading from a few dead individuals to others may be the cause, but this has not been established. Various worm parasites have been observed but their incidence is low.

GEOGRAPHICAL ASPECTS OF THE CLAM INDUSTRY

The east coast of the United States may be roughly divided into three sections as far as the clam industry is concerned. From Cape Ann north and east the soft clam is the predominant species of shellfish and is dug largely for commercial purposes. Here the tide range of eight feet and more exposes extensive flats which are generally protected from the open sea, thus providing ideal conditions for clam growth. The small size of the coastal communities where employment may be seasonal or occasional leads the inhabitants to depend heavily on the sea for at least part of their income.

Between Cape Ann and Cape Cod similar conditions exist in many localities. Where clams are plentiful, particularly in small communities, clamming may be performed mainly for commercial purposes. In this section digging for recreation and home consumption takes on some importance. Permanent employment in manufacturing and industrial plants reduce the necessity for de-

pendence on sea products, and as a result coastal inhabitants tend to consider shellfish resources as a means of supplementing their own diets rather than their income.

South of Cape Cod the oyster and quahaug supplant the clam commercially. The small tide range and difficulty of clamming in submerged beds make commercial exploitation of other species more profitable. The soft clam, however, plays a very important part in this section where inhabitants of heavily populated communities find it profitable to supplement their diet, particularly when there is considerable unemployment. It is estimated for example that 90% of the clams dug in Rhode Island are consumed either by the families of the diggers or by local inhabitants who purchase them direct from the diggers or through small dealers. The presence of clams also adds to the attractiveness of summer resorts. Tourists and vacationers expect sea food and the pleasure of catching it themselves.

Maine leads in commercial clam production with a yearly average of over six million pounds of meats. Massachusetts is second, averaging about three million pounds per year of which the greater part comes from the Ipswich and Essex region. In New Hampshire contamination of the Great Bay area has eliminated the most productive digging so that practically no clams are dug for commercial purposes. Rhode Island, in spite of its small commercial crop, probably ranks third in total production. Since 90% of this is for home consumption, it is apparent that clams must form an important item in the food budget of the inhabitants of that state. Contamination and unsuitable coast line generally limit commercial clamming in Connecticut, New York, and New Jersey.

ECONOMIC ASPECTS OF THE CLAM INDUSTRY

It is very difficult to evaluate the importance of the clam industry in the economy of coastal communities because few records are available which show how much individual clam diggers actually earn. In most states the shellfish resources are controlled by individual towns, each of which has its own system of licensing and restrictions with no obligation to make reports to a centralized authority.

In Maine however, new legal measures have recently been instituted which require that commercial clam diggers obtain a state license as well as local permits. This promises to facilitate the evaluation of the industry in the future. The Maine Department of Sea and Shore Fisheries has also maintained a competent staff of field workers who have kept in close contact with the clam industry for some time and have been able to make fairly accurate estimates on the number of active commercial diggers.

Information supplied by this department shows that clam digging at best can be considered only a part-time occupation. The average earnings are given in the following table.

Year	Estimated number of licenses	Average yearly earnings per license
1942	1,100	$427
1943	1,250	476
1944	1,500	276
1945	1,500	518
1946	1,875	968
1947	no information	.. ..
1948	3,335	536

It must be understood however that the term "average yearly earnings" is derived by dividing the value of the crop by the number of license holders. It is highly probable that some diggers take advantage of their licenses only occasionally to supplement their incomes or food supplies when other occupations are unavailable or unattractive. However these average earnings are so small that few diggers make a living wage by clamming alone.

Information derived from two towns on Cape Cod indicates that a similar si uaton exists in that part of Massachusetts. Average yearly incomes for persons in the towns of Barnstable and Chatham who hold commercial licenses for the taking of all types of shellfish are given in Table I.

A typical picture of the economics of clam digging has been obtained from the activities of industrious commercial diggers who depend on clamming for the greater part of their incomes. The writer has had the opportunity to observe two men digging in Barnstable harbor during the summer and fall of 1947. These two men, who were the only regular diggers out of several commercial license holders of the town, were out on the flats each day the weather permitted. Both were able to secure the two hods (1 1/5 bushels) limit allowed by the town regulations in spite of the extreme scarcity of clams. For their day's labor they were able to shuck out about two gallons apiece which were sold to local restaurants for about six dollars a gallon. They were able to work a total of about half the year, which would give each an income of nearly $2000 from clamming alone. This was supplemented by scalloping in the late fall and winter, but no observations were made on this activity.

The meager data presented above shows that clamming is generally an occasional occupation and in spite of present high prices, the most industrious diggers can hope for only a relatively small income.

The seed clam industry of Massachusetts is of special interest because it utilizes contaminated stocks which would otherwise go to waste or be bootlegged into food channels. Bonded master diggers are licensed by the Department of Conservation to employ diggers who may work over contaminated areas to supply seed clams for state shellfish aid and for sale to private grant holders. In 1947 master diggers in the Boston area were delivering seed in 20 barrel lots for $7 a barrel. (At this time the Boston fish markets were paying

as much as $18 a barrel for clean clams.) Diggers were paid $5 a barrel by the master diggers and were able to dig about two barrels a tide. Most diggers made at least $10 a day when they worked, and the master diggers made $40 a load minus the costs of transportation. This occupation however, cannot be depended upon to provide year round employment since the demand for seed clams is governed by the activities of the State Conservation department and of a few private grant holders.

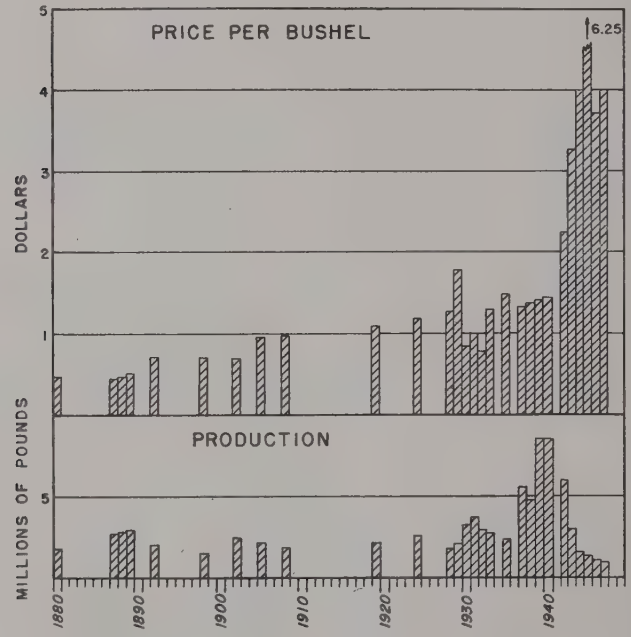

Figure 3. Massachusetts soft-shell clam statistics.

The overall value of the clam industry is difficult to evaluate. Besides the diggers, there are also involved the shuckers, canners, distributors, and restaurant owners. The Commissioner of Sea and Shore Fisheries in Maine has stated that he estimates the total yearly value of the clam industry in that state to be about seven million dollars. No other such estimates have come to the attention of the writer.

The value of the industry in Massachusetts is indicated by the imports of six of the largest dealers in the first 11 months of 1947. These dealers re-

ported to the Massachusetts Special Legislative Commission for the Study of Shellfish that they had imported from Maine and Canada 1,800,000 gallons of shucked clams valued at $9,000,000.

In addition to the industrial value in the strict sense, the availability of clams for clam bakes, in seafood restaurants, and for recreative digging provides an added attraction in resort communities and thus has a definite but indirect effect on their prosperity.

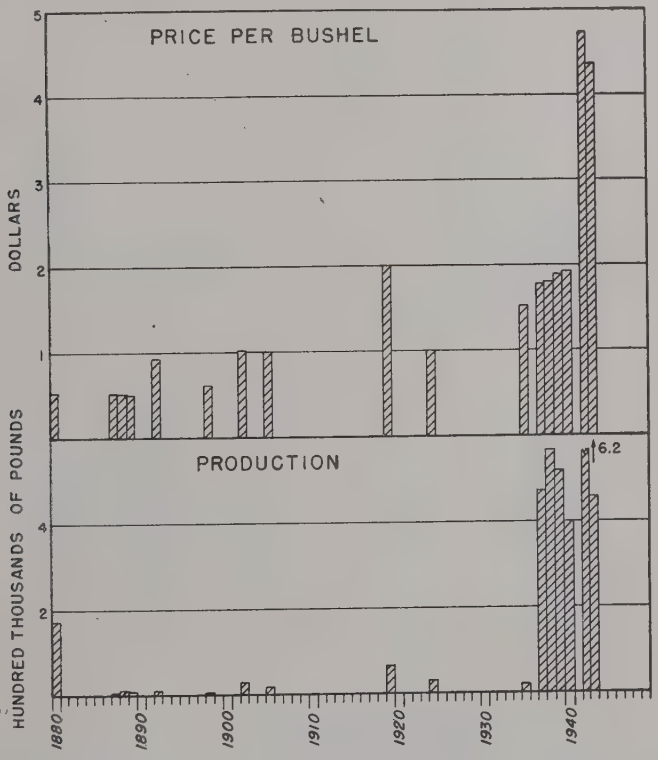

Figure 4. New Hampshire soft-shell clam statistics.

TRENDS IN CLAM ABUNDANCE

A unanimous opinion prevails among the coastal inhabitants that clams have been sharply declining in abundance for a number of years. Reports of

Kellogg, Mead, and Belding written in the early part of this century show that this opinion was held even at that early date. Actual trends in clam abundance are difficult to demonstrate because of the questionable reliability of the available statistics and lack of data on digging effort. The occasional nature of clamming as an occupation further complicates the picture. When prices are high there may be a greater tendency for coastal inhabitants to go clamming. When clam prices are low other employment may be more attractive even when clams are abundant.

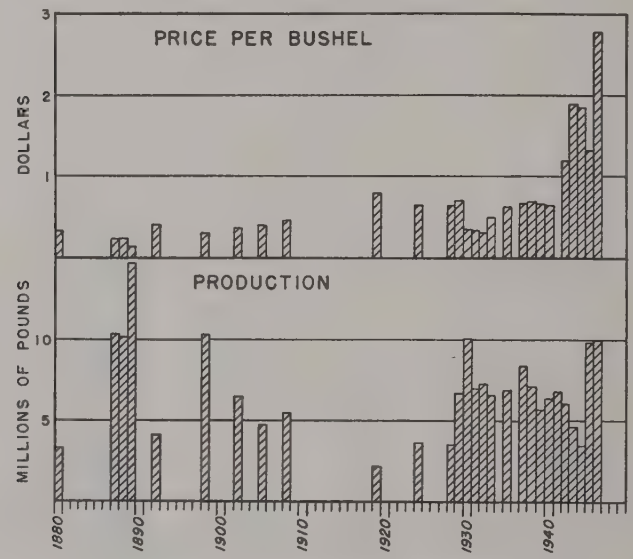

Figure 5. Maine soft-shell clam statistics.

The scattered statistics for Massachusetts for years previous to 1935 indicate a steady production of approximately three million pounds per year as is shown in Figure 3. Between 1935 and 1941 digging was intensified to satisfy the market which expanded as popularity of the fried clam became more widespread. During this period production tripled. After 1941 production declined sharply so that in 1947 the yearly production was no more than a million pounds. Two factors are suspected of influencing the decline. Larger areas were found to be polluted and closed by the Public Health authorities and intensified digging of flats which were not closed held the stocks down to a low level.

The yearly production figures for Maine shown in Figure 5 do not indicate any steady downward trend in clam abundance. The data for the last twenty years when the records were most complete demonstrate fluctuations which may be cyclic in nature, but the general trend is steady. Many of the high and low points are undoubtedly a result of economic factors which may stimulate or discourage digging by the presence or absence of more attractive

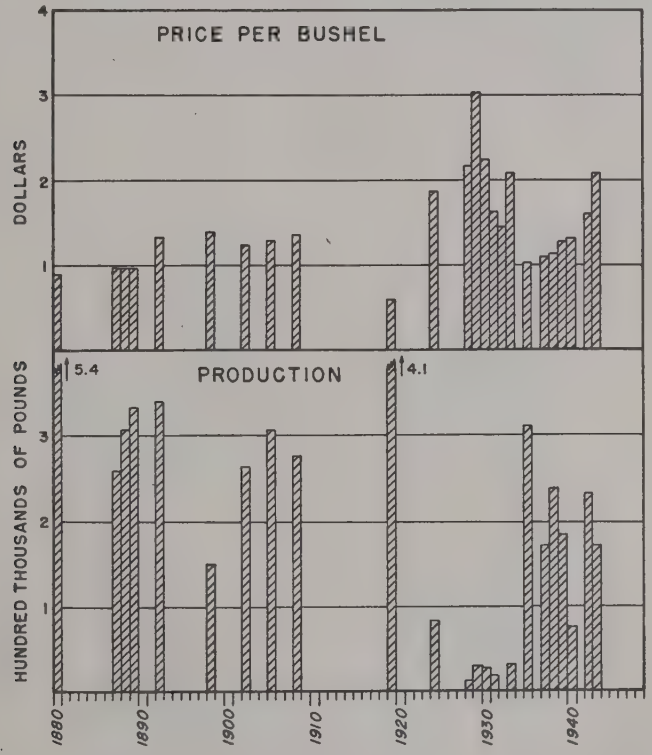

Figure 6. Rhode Island soft-shell clam statistics.

employment. The low point in 1944 may well have resulted from curtailment of digging by wartime activities, since production rose in 1945 and 1946 when military and civilian war work slackened.

In states south of Massachusetts little can be learned from the catch and price statistics which are shown in Figures 6 through 9. The industry is small in these states and unreported digging for local consumption is so extensive that it is impossible to determine abundance trends with any accuracy.

ATTEMPTS AT SHELLFISH IMPROVEMENT

EXPERIMENTAL PLANTINGS

The first records of experimental plantings were published between 1901 and 1904 by Mead who performed a series of experiments under the auspices of the Rhode Island Fish Commission. A number of tidal flats were closed by act of legislature for the purpose of making experiments on clam culture. Because of interference by poachers only one of several experiments was carried to conclusion.

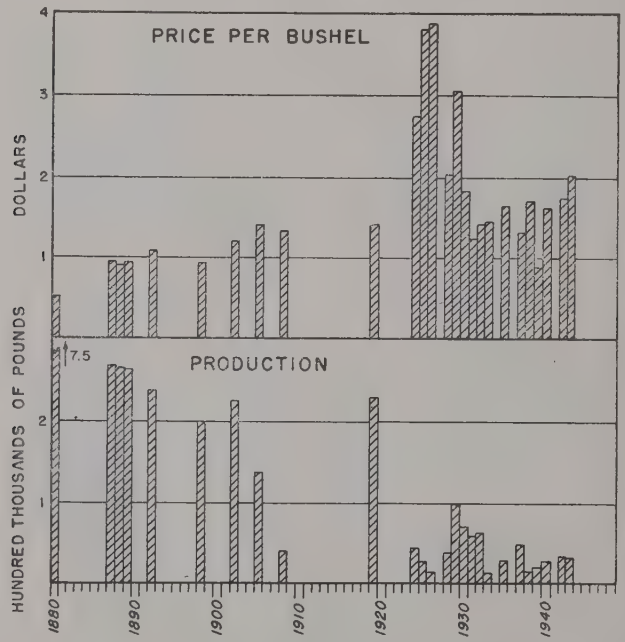

Figure 7. Connecticut soft-shell clam statistics.

Seven bushels of seed clams less than ½ inch long obtained from locations where heavy sets had occurred, were planted by scattering on a plot about 2/5 acres in area at a rate of 17½ bushels per acre. This area was then closed for two years. At the end of this time the clams had grown to between two and three inches in length and the area was opened to the public. Careful

samplings of small areas by the investigators indicated that the plot should contain about 3000 bushels per acre. However, estimates made on what was actually obtained from the plot by the public was about 1500 bushels per acre.

TOWN PLANTINGS

During the depression years several towns in Massachusetts took advantage of federal funds to plant seed clams on their depleted flats. This gave employment to needy persons and rehabilitated their shellfish resources at the

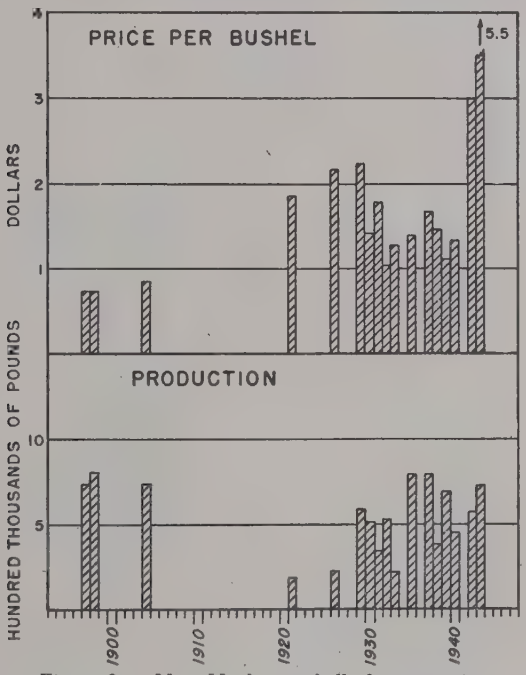

Figure 8. New York soft-shell clam statistics.

same time. A number of such projects which were started in 1934 were so successful that they were continued even after federal subsidizations were discontinued. See Table II.

Although records of these operations are not readily available, a great deal of valuable information has been obtained from town reports and personal interviews. The data presented may be questionable in connection with the return derived from each project since there is no way of checking the accuracy

of the various estimates. The cost of plantings was often partially subsidized by federal and state grants in amounts which seldom appear in town reports.

The general procedure is as follows. Seed stock averaging 1¼ inches is dug in contaminated areas by men licensed by the Conservation Department. Digging is often done on a morning tide and the seed is shipped by truck in ½ bushel bags to the town the same day. Some sort of supervision is required to prevent diversion of this contaminated material into food channels. Care in handling after delivery depends on the town shellfish officer who then transports the seed bags by boat to the flats and if the tides are unfavorable, sinks

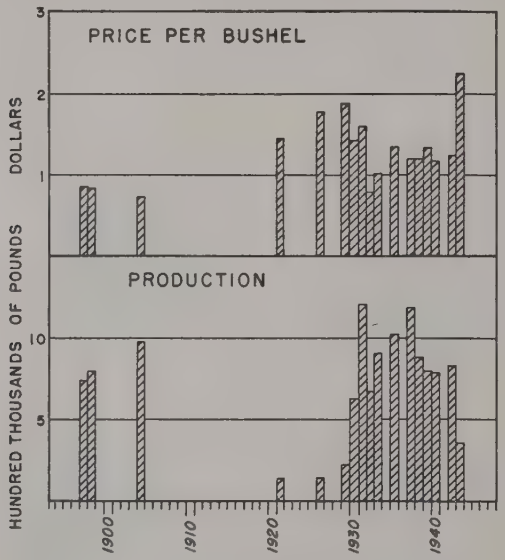

Figure 9. New Jersey soft-shell clam statistics.

the bags at high tide near the location where the planting operations are to be carried out. At low tide planting is accomplished by plowing in. As a rule one man plows a furrow with a hand plow and the seed is distributed by two others as in planting potatoes. A second furrow is then made covering the seed in the first furrow. This process is continued until the seed is all planted.

The efficiency of such operations is as follows. The quality of the seed is variable and is usually accompanied by a high percentage of shell and debris. Samples taken from deliveries at Barnstable in 1947 showed that as much as 40% by volume may be useless. Some of this is broken seed which results

from crushing in bottom layers of bags which may be piled too high in the delivery trucks.

After planting, the beds are often tended by deputy shellfish officers who collect and destroy such enemies as are obvious. Boring snails and their eggs, and small crabs are usually collected in pails and deposited on town disposal grounds. Large horseshoe crabs are pierced several times with a clam hoe and the shells broken. Part of the cost of control of clam enemies is borne by the state Conservation Department which allocates special funds for this purpose.

The data given in Table II suggest that cultivation of clams can be a highly profitable venture. These operations are often successfully carried out on flats which never or very seldom become populated by natural sets. This demonstrates conclusively that barren areas may be made productive merely by utilizing seed from contaminated areas which would otherwise go to waste.

It is also apparent from the tables that operations are usually carried out on a very small scale. Towns which possess many acres of barren flats seldom cultivate more than a very small proportion of the available area, largely due to the cost. In Massachusetts town money is appropriated from town funds for expenditures on shellfish propagation. Since the income from clammers' licenses and dealers' permits does not make up a significant fraction of a year's expenditure, the expense is borne by all the taxpayers of the town. When the clams are ready for digging, the profit is made only by the licensed diggers, who have contributed at most a few dollars in permits and taxes.

It would appear logical that if the industry is to be expanded to its fullest capacity, license fees should be adjusted to cover the principle costs of the plantings.

It was noticed when this information was being collected that a number of failures which may have occurred in town plantings were not recorded since shellfish officers were reluctant to report poor results in town reports. Present knowledge is sufficient to make it possible to recognize certain flats as unsuitable. Wave swept beaches of coarse sand are too shifting and clams planted in them may be either washed out or smothered. Accumulations of very fine silt have been reported as unfavorable in some sections in Maine. Investigations now in progress by the New York State Conservation Department indicate that certain soils cause death of clams possibly because of an unknown substance.

However, it is possible to check a locality for its ability to support clam growth. A few small experimental plantings may be made at small cost and will show whether the locality will support clams and what sort of production may be expected. If done in the spring useful information will be obtained by the end of the summer.

SPAT COLLECTING

It is a matter of general knowledge that intense sets of clams often occur in certain isolated localities leaving large tracts either entirely barren or very sparsely populated. It has also been noted that such sets do not necessarily occur in the same place in successive years. Several investigators have studied the conditions which influence setting.

One of the first studies on the conditions influencing the set was made by Kellogg in 1899. He observed a heavy set in the West Falmouth Harbor in a locality which later proved unsuitable for growth. After studying various environmental factors he concluded that the set was caused by the action of the tidal currents. Water rich in clam larvae rushed through the narrow harbor mouth then slowed down as the inlet widened. The current velocity also decreased from the center of the stream toward the shore so that larvae carried in by the rising tide were concentrated in the quieter waters where they could settle to the bottom.

Belding reported a heavy set which occurred in 1906 on Rowley Reef, Plum Island Sound where a horseshoe-shaped sand bar obstructed a swift current and formed an eddy. The bottom encompassed by this eddy which was about 50,000 square feet in area contained small clams averaging nearly 2,000 per square foot in number.

In 1902, Mead observed that in the Rhode Island waters, setting was patchy although larvae seemed to be abundant in the water at all times during the spawning season. After observing under the microscope that clam larvae would stop swimming and settle whenever they struck an object, he devised a spat collector which consisted of a box partially filled with sand and covered with a coarse wire screen. He reasoned that larvae would strike the screen and fall through into the box. This device was reported as being very successful even in localities where sets did not occur around the outside of the box.

Resurfacing unproductive flats has been observed to induce setting although the mechanism is not understood. Belding reported a heavy set occurring on flats formed from the dredgings of the Annisquam River in Gloucester, Massachusetts in 1905 and a similar occurrence in Yarmouth in 1920.

The operations of Marcus Howes of Barnstable are of special interest although he published no records. Mr. Howes resurfaced a portion of a ten acre grant with thatch sods and fine sediments taken from nearby thatch islands in 1911. He claims to have obtained successive heavy sets on this treated area and that sales grossed approximately $20,000 per year. One man who dug for Mr. Howes testified that he was able to dig as much as eight barrels per day, and that the producing area was sharply deliniated by the boundaries of Mr. Howes' grant. In 1926 renewal of the grant was refused by the town officials. At the present time, opinion is divided as to whether this area was made productive by treatment or was favorably situated for natural seeding.

It may be concluded that heavy sets occur to some extent where mechanical agencies in the aquatic environment concentrate larvae and allow them to settle. Whether setting is induced on resurfaced areas by a chemical stimulus or whether the physical nature of the sediments is responsible is not known.

CONTROL OF CLAM RESOURCES

The fundamental principle upon which the shellfish laws of most states are based is the free fishing right of the public in all marine waters below the high tide mark. As a consequence of this principle, there has been a tendency in all the New England states except Rhode Island to delegate control of intertidal shellfish resources to the various local communities. However, within the last few years when sanitation and conservation problems became more important, some state authorities have begun to assume more control.

Regulations pertaining to sanitation are fairly uniform in all the clam producing states and are based on standards laid down by the U. S. Public Health Service. These regulations define contaminated areas, minimum sanitary standards for processing plants, and transportation conditions. In each state a department or bureau competent to deal with the problems involved, is the authority. In effect such regulations remove the contaminated areas from local jurisdiction.

Conservation regulations are also commonly administrated by state authorities. A two inch minimum-length law is in effect in Maine, New Hampshire, and Massachusetts while Connecticut maintains a 1½ inch limit.

In addition, Maine and Connecticut have incorporated many of the town laws into state departmental regulations so that state conservation officers may be empowered to assist the local authorities in law enforcement.

Maine has recently adopted legislation requiring state-issued licenses of persons engaged in all aspects of the clam industry. The income from the license fees finances clam conservation programs and the records obtained promise to provide considerably more information about the industry than has hitherto been obtained in any state. The practice of state licensing of diggers was also enacted in New Hampshire with supervision of the clam flats delegated to the conservation officer in 1941, but was repealed in 1944 because of a clause which required a residency of five years and thus deprived summer residents of the privilege.

Local regulations are generally concerned with conservation as it pertains to the local situation. Daily limits are common in all coastal communities where a scarcity exists. In Connecticut many towns have increased the minimum length to two or two and one quarter inches. Closed seasons are also common. In addition, many communities issue regulations designed to restrict the benefits derived from their shellfish resources to local interests. Some towns limit digging to their own residents. Others with a profitable resort trade restrict or prohibit exportation of shellfish in order to maintain a supply for local consumption. This is carried to extremes in the four eastern Maine counties where exportation of the clams beyond the limit of the state or into any of the western coastal counties during the summer is prohibited. Since clam canning is restricted during this period because of the post spawning drop in meat yield, this law is presumably designed to prevent depletion of the flats during the sum-

mer when the demand for fresh clams is great and thus preserve an adequate supply of clams for canning in the winter and spring when the meat yield is high.

Regulations which provide for individual initiative in clam culture are in existence in Maine, Massachusetts, New York, and New Jersey. In Maine residents may acquire intertidal land for shellfish culture from either the town or state. Towns are prohibited from granting more than ¼ the area of the available flats and the state may grant ½ acre. Preference is given to the riparian owners of the adjacent properties and public hearings are required before grants are made. Opposition of the general public has prevented much development of individual shellfish culture. In Massachusetts the authority to make intertidal shellfish grants is vested in the selectmen of the coastal towns who may grant as much as five acres of barren flats to town residents for clam culture. The term "barren" is defined as flats which have not produced an appreciable shellfish crop in the two years previous to the time of granting. Public hearings are required before action is taken on applications for grants. Here also there is considerable public opposition although a recent reversal of public policy in the town of Barnstable has made it possible for 18 residents to acquire grants of 5 acres each. The Massachusetts law requires that grantholders develop their areas to contain $25 worth of clams per acre within two years. Thus riparian owners of shore front properties are prevented from acquiring clam grants merely for the purpose of preventing trespassing on their intertidal beaches.

In New York, the ownership of intertidal land varies according to the charter of the individual community. In some towns, the low tide mark is the seaward boundary of private property. In others the intertidal zone is controlled by the town. Certain of the flats of the Long Island bays come under state jurisdiction. Consequently individuals wishing to obtain clam grants must approach whatever authority maintains control. The few instances of attempts at clam culture have not met with success because of unsuitable grounds.

The reluctance of legislative bodies to deprive the public of its fishing rights by closing intertidal flats has even restricted state development bureaus and commissions from carrying out research. Special legislation was required in Rhode Island in 1901 to permit the commissioners of fisheries to occupy flats for the performance of experiments on clam culture and the area was limited to three acres. In Maine the Sea and Shore Fisheries Department is limited to two acres in any one location but larger conservation areas may be established by agreement with the towns. The Massachusetts laws permit the director of Marine Fisheries to control "not exceeding ten ponds and estuaries, creeks or other arms of the sea—" for purposes of scientific investigation of all fish.

POLLUTION PROBLEMS

The soft clam producing area of the east coast has probably been more seriously affected by domestic and industrial pollution than by any other factor. Within the past 40 years during which minimum sanitary standards have

become standardized, the clam industry has been completely eliminated from some areas.

The discharge of industrial wastes into rivers, estuaries and harbors may render the waters unsuitable for the growth of marine invertebrates and thus prevent setting and growth of clams on flats which might otherwise be productive. Domestic pollution on the other hand, may actually provide better conditions for clam growth by increasing the food supply. However, the danger of epidemics of gasto-intestinal diseases such as typhoid, dysentery, and others has caused the public health services in every state to adopt the recommendations of the U. S. Public Health Service and prohibit digging in all areas where the incidence of pollution is too high.

The index of pollution generally accepted is the most probable number (MPN) of human intestinal bacteria found in 100 milliliters (approximately 0.1 quarts) of clam meat and shell liquor. The U. S. Public Health Service recommends that clams whose MPN exceeds 2,400 be considered unfit for human consumption. It must be understood that the bacteria are not in themselves pathogenic except in rare circumstances, but their presence in large numbers indicates that clams are accumulating large quantities of human intestinal wastes in which there is danger that disease-causing bacteria may be found. For this reason many coastal inhabitants have eaten clams from polluted areas for years and have suffered no ill effects when none of the contamination was discharged from the homes of carriers of typhoid or dysentery. These people are inclined to resent the closure of their digging grounds since they do not realize what the consequences would be if persons carrying intestinal disease should move into their areas.

Close approximations as to the effect of pollution on the clam industry are available only for New Hampshire and Massachusetts. The Great Bay area of New Hampshire which has become progressively more contaminated by the Piscatequa river was entirely closed to digging by 1940. A drastic drop in production in the two other clam producing areas in the state for reasons other than pollution has rendered the industry practically non-existant.

More detailed information is available for Massachusetts. Fortunately a complete survey of the clam producing areas was conducted in 1907 and estimates were made of the productivity of the different areas. By comparing this information with recent pollution charts it has been possible to estimate the reduction of clam producing flats with a fair degree of accuracy. Table III shows that the 5,111 acres which were producing in 1907 have been reduced to less than 2,000. Furthermore, 6,096 acres which were potentially capable of growing clams in 1907 have been reduced by nearly one half. In addition, the Salisbury-Newburyport flats combined with the Lynn-Saugus areas produced half the clam crop of the state in 1907 and are now totally closed.

Information on the extent of pollution in Maine is less quantitative but indicates the trend for that state. A survey conducted in 1938 indicated that 58 localities of unspecified area were closed. It was estimated at first that

this area included 20% of the flats and 40% of the best digging. A survey now in progress indicates that this estimate is probably somewhat exaggerated and the situation is much less serious. In addition, further investigations have made it possible to open 4 areas and reduce the extent of eleven others. Seven areas have also been opened up for winter digging when the incidence of pollution is low in the absence of large summer populations.

The wide extent of contamination of the waters of the Southern New England and Middle Atlantic states is due to the intensely populated industrial communities. It has not been possible to secure information on the effect of pollution in these regions.

In Massachusetts where over 60% of the clam producing flats have been closed because of pollution, an attempt has been made to utilize these resources by purification with chlorine. Three cleansing plants have been operated for several years with some success. The general practice is to hold the contaminated clams in sea water containing from 0.2 to 0.5 parts for million residual chlorine for twenty-four to forty-eight hours. This procedure reduces the coliform count of the shell liquor 75 to 90 percent. Thus clams containing no more than 24,000 bacteria may be successfully processed to reduce the count of coliform bacteria below 2400 per 100 ml.

In 1945 some difficulty arose because of a decision by the United States Public Health Service that the entire clam body instead of the shell liquor should be used in determining the degree of pollution. It was found that the clams would circulate water freely in the presence of small chlorine concentrations but would not feed or eliminate bacteria already concentrated in the gut. As a result, cleansing with chlorine was considered usatisfactory except for clams which were very lightly polluted.

The Massachusetts Public Health Department has been recently carrying out experiments on cleansing polluted clams with clean sea water. The preliminary results indicate that this process may be vastly superior to the chlorine method and that it may be possible to purify clams from grossly contaminated areas where coliform counts exceed 24,000. The method has one drawback however. Uncontaminated sea water is usually not readily available in regions where cleansing plants might best serve and shipment of contaminated clams to distant plants would add to the cost of operation. Consequently investigations are now being carried on to test the efficiency of using water which is first sterilized with chlorine and later has the chlorine removed chemically.

PRESENT PROGRAMS

INVESTIGATIONS

At the present time, investigations of various clam problems are underway in the Maritime Provinces of Canada, Massachusetts and Maine.

In Massachusetts an intensive program of investigations is being conducted in Barnstable harbor by personnel of the Woods Hole Oceanographic Institution. Methods of planting seed are being studied, and factors which may

induce setting are being investigated. Several private individuals have secured grants of five acres each and their operations are being conducted in close co-operation with the investigators. Investigations of the waters, soils, and other environmental conditions are also being conducted.

In Canada*, the Atlantic Biological Station is conducting studies to show how growths and survival of transplanted 1½" seed stock are affected by density of crowding and by different methods of handling and planting; how yield, year after year, in bushels per acre of naturally populated areas is affected by various methods of harvesting; how yield of meats in pounds per bushel is influenced by season, environmental factors and by various commercial handling methods. The usefulness of stunted stocks for seeding barren areas is being tested and the biology of certain clam enemies is also receiving attention.

Preliminary results on growth rates in this region have shown that in most of the producing areas five years or more are required before clams reach commercial size and therefore it is doubtful that clam farming on a commercial scale could be profitable in Canada except in those inlets where the most favorable conditions for growth and survival obtain.

Growth rates of transferred stock have been shown to be less at high than at low levels on the beach, less for stunted than for "normal" seed clams, less in sheltered parts of inlets than where water circulation is active and, in certain soils, less when the soil is undisturbed than when it is periodically loosened by digging.

Annual natural mortalities in transferred stocks which survive the planting operation in good growing areas vary greatly, being sometimes as low as 2% in sandy soils and as high as 15% in clayey soils. Stunted stock appears to survive just as well as normal. Digging for large clams may destroy a high percentage of the small young clams that are left in the soil by burial and smothering at depths that are too great to permit them to recover their normal position near the surface. This mortality is highest in clayey soils where it may involve 60% of the one- and two-year-old clams.

The yield of meats per bushel of shell stock improves when the soil in areas that have been undisturbed for long periods is loosened by digging. It increases toward the mouths of inlets, towards the lower inter-tidal levels, as the density of crowding decreases, as the size of commercial clams decreases and when the time interval between digging and shucking is reduced. It is highest just before spawning and lowest in the immediate post spawning period and it changes little during the winter months.

Studies of two boring snails *Polinices heros* and *Polinices triseriata* have shown that the former is less numerous and probably less destructive than the latter. *P. heros* has been shown to have a free swimming larva while *P. triseriata* emerges directly from the egg case as a crawling snail. This suggests

*Information concerning Canadian activities was supplied by Dr. J. Carl Medcof, Shellfish Biologist for the Atlantic Biological Station, St. Andrews, New Brunswick.

that partial control of the latter species by destruction of egg cases may be possible, and this is being tested. Predations by these two species may be so great as to completely destroy transferred stocks of 1½" seed clams or natural sets of clam spat in badly infested areas within a few months. Attempts to reduce the infestations of *Polinices triseriata* in experimental plots by manual collection of adult snails have shown that this is not effective as a control measure because the animals are nocturnal and very numerous (up to 15 per square foot). Only a small proportion of the population comes to the surface at any one time and even then the smallest snails which are most destructive because of their greater numbers, usually escape the notice of collectors.

Studies of the efficiency of various methods of harvesting natural populations and the effects that these methods have on sustained yield per acre are still incomplete. They include a comparison of "systematic" digging where all the soil is completely turned over once a year and levelled off after digging by crews of men working abreast, as opposed to "random" digging where the men work wherever and whenever they choose. Another experiment is designed to test the yield of various plots when dug systematically, twice a year, once a year, once every second year and once every third year.

In Maine an ambitious program of investigation is being conducted by personnel of the Department of Sea and Shore Fisheries. By agreement with the town of Scarboro, seven conservation areas have been established and seeding arrangements have been made. The town has set a license fee of $25 with a remittance of $20 to each digger who brings in three barrels of seed clams for use on the conservation areas. The available seed includes newly set stocks which occur in too great concentrations for optimum growth and also stunted material which is found at levels too high above the low tide mark. A somewhat similar program is under way at Harpswell. In addition numerous similar programs are being contemplated as agreements with various towns can be reached.

The salvaging of stunted clams which occur in large numbers is also receiving attention. Studies of shell - meat ratios are being made in cooperation with commercial canning firms. The legal aspects of taking undersized stunted stocks is under consideration.

The Department of Sea and Shore Fisheries has also made cooperative agreements with other state departments which will make personnel and equipment available for a topographic and geological survey of the intertidal lands between Bath and Friendship this coming summer. If this information shows promise in interpreting factors affecting clam growth, the survey may be expanded to include the entire coast of Maine.

Flats now closed because of pollution are examined from time to time to determine the clam population and also the likelihood of reduction of contamination. Such examinations have made possible the shifting of pollution lines and the opening of good clamming areas for winter digging.

In addition, new legislation has been instituted which provides the central authority with funds and more control. Provision is made for more accurate statistical studies by which the entire industry may be better evaluated.

CONSERVATION PROGRAMS

The maintainance and management of conservation areas in Scarboro, Maine are part of a conservation program as well as one of investigation. These areas will ultimately be opened for public digging and will benefit the diggers of the town.

A similar conservation program has been under way in Massachusetts for some time. The Department of Conservation is empowered to supply seed clams to such coastal towns as defray half the cost. Many towns have taken advantage of this opportunty including those mentioned in a previous section. In addition the Conservation Department has funds with which to assist coastal towns in management of the beds and elimination of clam enemies.

DISCUSSION

PRESENT CLAM SITUATION

Biological knowledge. The present knowledge of the biology of the clam is based almost wholly on the works of Kellogg, Mead, and Belding. These investigators have given a rather complete picture of the life history and have made several preliminary contributions to our knowledge of the ecology and physiology of the clam. However, the precise conditions which influence spawning, setting, and survival are in need of more intensive investigation. The role of soil types, enemies, and epidemic mortality on clam populations has never been clearly determined nor have methods of control been properly valuated.

Shellfish officers and interested persons have acquired a considerable fund of practical information which pertains to various local situations. This sort of information deals with methods of transplantation, care of beds, and predator control. In general, this knowledge is not available through publications, and considerable difficulty may be experienced in obtaining the information because of the absence of exact records. Procedures used by local authorities are also the "rule of thumb" variety which have been developed by trial and error without exhaustive scientific testing.

EXTENT OF THE CLAM RESOURCES

There is probably less known as to the extent of the clam resources of the northeastern states than any other resource of similar value. There is no published material which contains records of the areas of the producing and potentially producing flats or even of the areas closed because of contamination. For purposes of this report the potential area of Massachusetts has been calculated from a recent sanitary survey combined with a shellfish survey which was completed in 1907. The resulting figure of 5,000 potentially productive acres is based on the assumption that no changes have occurred since 1907. A considerable body of local opinion holds that natural causes have reduced the productive area in some regions. If this is true the foregoing assumption is not valid.

Trends in clam populations are also subject to considerable controversy. Personnel involved in the industry are in nearly unanimous agreement that the clam resources have been dwindling and that depletion from overdigging and natural causes has reduced the present populations to low levels. However, production statistics do not generally demonstrate this for any state except Massachusetts. Maine's yearly production fluctuates violently from year to year but the general trend has remained relatively constant since 1889. In the Middle Atlantic and Southern New England States where the majority of the clams dug are believed to be diverted into small businesses and home consumption, neither of which contribute to commercial statistics, it is impossible to demonstrate trends in abundance.

The available evidence suggests that current digging effort stimulated by high prices is of sufficient intensity to harvest each generation of clams as soon as they grow to legal size. This can produce an apparent depletion even though the total numbers of each generation may be as great as they ever were. Unfortunately statistics from which digging effort may be calculated have never been collected.

PUBLIC OPINION AND THE PRESENT LEGAL SITUATION

Current legal measures affecting clams and the clam industry are somewhat chaotic. The trend toward centralization and unification of the shellfish laws in Maine shows definite progress. Here greater jurisdiction is being assumed by the Department of Sea and Shore Fisheries which is an agency sympathetic with problems of the industry and is also one which holds the confidence of the fishermen.

In Massachusetts control of the shellfish resources is now distributed to the towns. Here the character of the coastline is so complex and the problems of the shellfish industry so diversified that unified regulations may not be advantageous to the industry.

For many years the shellfish resources have been considered as public property and a definite negative attitude toward any kind of conservative management prevailed. As shellfish products become more in demand and it is becoming apparent that the supply is not unlimited, public opinion appears to be changing gradually in favor of positive action to conserve the resource. As a result, community shellfish improvement programs have been instituted in certain Maine towns, and on Cape Cod interest in improving barren areas by public and private effort has developed. Accompanying the awakening to the need for definite programs, has come the realization that there is insufficient knowledge of the biology of the clam to provide a concrete basis for intelligent improvement programs. Consequently measures to provide for investigations have been initiated by popular demand in the legislative bodies of Maine, Massachusetts, and the Federal Government.

PRESENT NEEDS

It has been shown that under the free fishing system the shellfish producing areas are unable to provide enough soft shell clams to satisfy the ever growing demand. It is apparent therefore that there is a definite need to increase the productive areas. At the present time there is evidence that the following measures would each contribute to this end:

1. Planting seed clams where sets do not normally occur. On the Massachusetts coastline this would nearly triple the productive area. Presumably this ratio prevails all along the New England Coast.

2. Creating new seeding areas by treatment of the surface. Evidence is accumulating that this method is practicable in certain localities.

3. Reduction of polluted areas. Over half the clam flats of Massachusetts are closed because of pollution. In many places the value of the shellfish crop would offset materially the cost of pollution abatement.

4. Utilization of clams from polluted areas by purification and as sources of seed. This has been carried out profitably on a limited scale in Massachusetts for some time.

5. Management of present productive areas for the greatest economic benefit. It is possible that existing clam beds may be made to provide a greater sustained yield if managed properly. In some localities greater benefit may be derived by reserving beds for digging for home consumption or as an attraction for summer vacationists rather than for commercial purposes.

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TABLE I

SHELLFISH INCOME

Barnstable

Year	Number of Licenses	Shellfish Income	Shellfish Income per Man
1935	396	$37,050	$93.56
1936	154	62,050	402.92
1937	320	107,900	337.18
1938	337	53,650	159.19
1939	263	64,050	243.53
1940	277	54,100	195.30
1941	59	54,900	930.50
1942	108	81,000	750.00
1943	130	140,200	1,078.46
1944	129	129,500	1,003.85
	2,173	$784,400	

Average income per man $360.97 per year.

Chatham

Year	Number of Licenses	Shellfish Income	Shellfish Income per Man
1942	318	$38,235	$120.23
1944	134	30,557	228.03
1945	114	22,134	194.15
1946	105	22,146	210.91
1947	146	17,008	116.49
	817	$130,080	

Average income per man $159.21 per year.

TABLE II

PLANTING STATISTICS

Barnstable

Date of Planting	Cost of Planting	Barrels Planted	Date Dug	Barrels Dug	Return
1934	$1,500.00	500	1935-36	1665	$6,825.00
June 1935		36	1935-36	85	425.00
June-July 1935		57	1936	75	379.00
?		242	1936	522	2,050.00
July-Aug. 1935	20.00	43	1938		1,000.00
June-July 1936	656.00	394.5	1938		2,724.00
May-June 1938	300.00	104	1939		489.00
			1942		2,119.71
Orleans					
1940	46.69		Aug. 1941		$450.00
Summer 1941	185.00		Nov. 1943		715.00
Eastham					
?	$400.00		1937		$1,880.00

TABLE III

COMPARISON OF PRESENT CLAM PRODUCING AREAS IN MASSACHUSETTS WITH THOSE OF 1907

TOWN	1907 Production bu.	1907 Productive Area acres	1907 Possibly Productive Area acres	Fraction of 1907 Productive Area Closed by Pollution percent	1947 Productive Area acres	1947 Possibly Productive Area acres
Salisbury	15,000	250	.. ..	100	.. ..	.. ..
Newburyport	55,500	1,080	.. ..	100	.. ..	.. ..
Newbury	300	100	260	50	50	130
Rowley	2,000	100	300	.. ..	100	300
Ipswich	25,000	820	125	25	615	100
Essex	15,000	300	325	.. ..	300	325
Gloucester	6,000	175	275	25	130	50
Manchester	100	5	10	100	.. ..	.. ..
Beverly	100	10	30	.. ..	10	30
Salem	200	15	70	100	.. ..	.. ..
Lynn	1,000	40	160	100	.. ..	.. ..
Saugus	1,000	50	100	100	.. ..	.. ..
Nahant	300	50	150	100	.. ..	.. ..
Boston	7,500	1,280	1,000	100	.. ..	.. ..
Cohasset	200	10	40	25	7	10
Scituate	200	20	40	.. ..	20	40
Marshfield	200	30	30	.. ..	30	30
Duxbury	700	15	800	.. ..	15	800
Kingston	500	10	150	50	5	50
Plymouth	3,000	60	440	50	30	100
Barnstable	700	20	330	.. ..	20	330
Yarmouth	600	15	25	.. ..	15	25
Orleans	3,000	75	75	.. ..	75	75
Eastham	4,000	75	100	.. ..	75	100
Wellfleet	800	15	250	.. ..	15	250

became depressed as much as two inches. During this period the planted clams became drastically reduced in numbers so that by August, few clams could be found. Digging failed to disclose any shells in the beds except for a few paired shells which had been drilled by boring snails. The absence of shell suggested that the clams were being eaten by organisms which destroyed the shells, and the large numbers of horseshoe crabs' burrowings, concentrated in the planted beds, made it seem logical that the horseshoe crab was the responsible predator.

A laboratory experiment was set up to test the predations of the horseshoe crab. A miniature clam bed was set up in a 9 x 13 inch photographic tray, partially filled with sand, and seeded with 100 clams averaging a little less than half an inch in length. One horseshoe crab measuring 3 1/16 inches at the greatest width was placed in the tray which was then circulated with running sea water for 72 hours. At the end of this period the sand was carefully screened through a standard screen with openings measuring 0.078 inch.

Only one clam was found intact. The others had been so thoroughly ground up that but few shell fragments, large enough to be retained by the screen, remained. It appears logical that if horseshoe crabs operate in the same way under natural conditions they could eliminate well populated clam beds rapidly, leaving no evidence except disturbances in the surface of the sand.

THE BORING SNAIL

Three species of boring snails are commonly found on the intertidal flats of the North Atlantic Coast. They are *Polynices heros*, *triseriata*, and *duplicata*. *Polynices heros* and *duplicata* are common in Massachusetts, while *P. triseriata* occurs more abundantly to the north.

The boring snail burrows down into the flats and wraps its foot around a live mollusc such as a clam or small quahaug. It then bores a countersunk hole through the shell, usually near the umbo, and sucks out the contents. The hole is bored with the radula, a rasp-like structure located in the floor of the mouth. When clams are deeply buried, the disturbance of the sand caused by burrowing of the snail is not great enough to cause the shells to be washed out so that pairs of shells of clams thus killed may be found by digging.

The amount of destruction caused by boring snails has been subject to conjecture for sometime. Belding estimated that a large snail could destroy about 26 clams a month. Medcof estimated that *P. triseriata*, a small species, occurred in sufficient numbers on the flats of New Brunswick to eliminate 90% or more of a new set. He further showed that control of these pests simply by picking them up was ineffective since only a small number were visible on the surface at any one low tide.

In the course of the clam propagation experiments at Barnstable, Massachusetts, some observations have been made on the effect of boring snails. It was first noticed that shortly after a set of clams had appeared on sods which were set out in the summer of 1947 as spat collectors, numbers of bored shells could be found among the grass and roots. It was not possible to make a quantitative estimate because many of the shells were washed away at each

tide since destruction was occurring before the clams had dug in. Later it was found that the only clams which had survived from that set were those which actually became imbedded in the roots of the sods where the snails were impeded from burrowing.

In addition, clams were found in another situation where they were protected from boring snails. In one locality, erosion of the surface had exposed pairs of shells of large clams which had died some time in the past. Many of these shells were found to contain one or two small clams although no other living clams could be found in the immediate vicinity. There were, however, numerous boring snails which were feeding on small razor clams and an occasional quahaug. Bored shells of the soft clam were also present.

It appears likely that predation of boring snails may be of sufficient magnitude to prevent the appearance of a set. Since clam diggers seldom recognize the appearance of a set until the clams are nearly half an inch long, destruction by snails of clams less than a quarter of an inch long would make it appear that no set had occurred.

CONTROL OF PREDATORS

At the present time an attempt is made to control predators on the flats of Barnstable and other towns by policing the planted beds and picking up and removing horseshoe crabs and boring snails to town disposal grounds. Survival studies made on the Barnstable public plantings indicate that this procedure is partially effective. A survey made in September 1947 of a bed which had been planted in May 1946 gave the following results:

48% by volume survived.
38% could not be found and were presumably destroyed at least in part by horseshoe crabs.
3% were killed by snails and the bored shells remained.
11% died from unknown causes and the paired shells remained.

Clams in this bed and others where predator control was in effect continued to survive and grow during the spring and summer of 1948 at the same time that planted beds which were not patrolled suffered almost complete destruction. However, this type of predator control is only partially effective as shown in the table above. It has the further disadvantage of being relatively costly.

APPENDIX III

FURTHER OBSERVATIONS ON PREDATORS OF THE SOFT-SHELL CLAM*

BY

HARRY J. TURNER, JR.
JOHN C. AYRES
CHARLES L. WHEELER

It has been demonstrated that predations of the horseshoe crab and the boring snail affected clam populations adversely. Observations made since that time have shown that the activities of three other predators, the green crab, the blue crab, and the fiddler crab may also be important.

THE GREEN CRAB

The green crab, *Carcinides*, ranges from Maine to New Jersey. It has appeared in great numbers in certain years on the extensive clam flats of Ipswich and Essex. Shellfish officers of this region claim that two of the worst years were 1932 and 1946.

The green crab works over the flats digging out and eating small clams in large numbers. Clam diggers claim that during years of heavy infestation these crabs are so numerous and bold that they even swarm over buckets of clams set down by the clammers during digging, and nip off any parts of the clams that are exposed, such as the necks and feet. No estimate has been made of the damage done to clams in the sand but it is believed that when numerous, green crabs may be able to practically eliminate new sets.

THE BLUE CRAB

The blue crab, *Callinectes*, is the edible crab which ranges from Cape Cod to Louisiana. It is an important commercial product in the Middle Atlantic States.

The blue crab is believed by clam diggers to be an important clam predator on the flats south of Cape Cod. Mead was unable to show that the blue

*This report was presented in preliminary form to the Committee of Clam Technicians sponsored by the Atlantic States Marine Fisheries Commission, October 5, 1948.

crab was a serious pest, but Belding was of the opinion that it could do serious damage to young clams.

In early October, the authors had an opportunity to observe a private shellfish grant in South Dartmouth, Massachusetts, under the management of Mr. Morgan H. Plummer. A portion of the grant had evidently obtained a heavy set of clams earlier in the summer, but the numbers of clams had dwindled except where Mr. Plummer had installed protective devices which will be discussed later. Small blue crabs and their diggings were in evidence everywhere, and occasionally one could be seen dislodging a small clam and crushing it with its powerful claws. There was no evidence of horseshoe crabs or boring snails in the vicinity.

THE FIDDLER CRAB

There are several species of the Fiddler Crab. *Uca*, which are generally considered to range from Cape Cod to the Gulf of Mexico. In recent years it has been observed on the north side of Cape Cod. The fiddler crab is an inhabitant of salt marshes or sandy beaches near the high-water mark where it lives in deep burrows. It does not generally migrate down the beach except at low tide.

There are no records of fiddler crabs preying on the soft-shell clam.

The authors recently observed fiddler crabs digging out and eating small clams on Mr. Plummer's grant at South Dartmouth, Massachusetts. Mr. Plummer, himself, stated that he had been watching the progress of the clam set for some time and was convinced that the fiddler crabs, which were very numerous, had done great damage.

DISCUSSION

At the present time there appears to be no information on the quantitative aspects of the predations of these organisms. Reports by the shellfish officers of Ipswich and Essex suggest that a considerable part of the shellfish problem in these areas is one of predator control. Attempts have been made at trapping the green crab in crab pots but no information as to the results has been compiled.

South of Cape Cod it would appear that the blue crab and fiddler crab may be serious pests since their combined activities cover a complete tide cycle, with the blue crab working at high tide and the fiddler crab at low.

An experiment performed by Mr. Plummer, the grant holder at South Dartmouth, has given some rather startling results which may suggest how beds of clam seed may be protected artificially. Mr. Plummer constructed some trays of galvanized ¼ inch mesh screen about 3′ x 6′ x 2″ and inverted them over some thickly populated sections of his flats. He worked the edges down into the sand so that the bottom of the trays were level with the surface of the sand. In early October, when the authors observed Mr. Plummer's

installations, clams were still present under the screen in large numbers. The densely populated areas were strictly limited to that protected by the screens and only an occasional clam could be found in the surrounding areas though broken shells were abundant.

It is, of course, apparent that the cost of protecting large areas with expensive galvanized iron screen would be prohibitive and that corrosive properties of sea water would make it necessary to renew the screen at frequent intervals. However, it is suggested that the use of more durable plastic screening might serve the purpose. It is reasonable to suppose that cold weather restricts the activities of predators so that protective devices might well be taken up during the winter when they would be damaged by ice.

APPENDIX IV

THE SOFT CLAM FISHERY OF MASSACHUSETTS

BY
CHARLES L. WHEELER

The purpose of this report is to discuss the soft clam resources in the various coastal towns of the Commonwealth and to show how these resources are managed in different localities. There are three major aspects of the soft clam fishery which determine its importance in any locality. 1) Clams may be dug by commercial diggers for export or sale to local restaurants. 2) Local residents may supplement their family diets with soft clams dug by themselves. 3) Recreational clam digging may be a feature which attracts vacationists and summer residents to the town.

These three interests may or may not conflict, depending on the extent of the resources, nature of the local population, and general economic pattern of the town in question. Management of the clam flats is usually directed toward reserving them for one or more of the above mentioned purposes. Commercial digging is licensed where extensive flats grow clams in sufficient numbers to make it a worthwhile occupation. Towns having a small vacationist trade and limited clam flats expect digging for family use to be the rule, particularly when there are seasonal unemployment problems. Still other localities which depend heavily on vacationist and tourist trade expect their clam resources to provide an added attraction and in this way resources which are too limited to attract the commercial digger become important in the economy of such a town.

The importance of the shellfish resources has been realized for some time. As early as 1905 the General Court authorized the Commissioners of Fisheries and Game to make an extensive survey of the shellfish resources of the Commonwealth and appropriated money for this purpose. The survey was conducted by their biologist, Dr. David L. Belding, and was completed in 1907. The results of the survey were published by the Commonwealth in

1909. No comprehensive investigations on shellfish problems of Massachusetts have been made since that time.

Throughout this report references are frequently made to the Belding report of 1907. It is indeed fortunate that this material was made available so that aspects of the present day fishery may be compared with those of this earlier date for the purpose of determining the trend.

The present report represents a preliminary survey of the coastal cities and towns of Massachusetts. A more detailed treatment of the subject is contemplated in which management of resources will be described at greater length. The following is more of a general description of the various sections of the Massachusetts coast than a study of individual towns and much has been omitted for the sake of brevity.

SALISBURY AND NEWBURYPORT

The clam flats at the mouth of the Merrimack River were once the most productive in the State of Massachusetts. In 1907 more than 70,000 bushels were taken from the waters of the two towns. The Newburyport area, located on the south bank of the river, covers 1,000 acres. Forty years ago 175 men derived at least part of their livelihood from this section and in Salisbury 250 acres were worked by 66 diggers.

Within the past decade this tremendous area has been completely closed because of the contamination of the Merrimack River by the industrial cities and towns along its banks. In 1948 a small section of the Salisbury flats was opened to digging provided that the clams so taken were processed at the nearby Plum Island shellfish purification plant. Most of the Merrimack clam grounds, however, are still lost to the industry and there is little hope of returning them to productivity until the river is at least partly freed from pollution. A survey of conditions along the Merrimack has been made and it is hoped that in the future disposal of industrial wastes and domestic sewage will be made in some other manner than by discharging them into the river. When this is accomplished, an extremely valuable resource will be given back to the towns of Salisbury and Newburyport.

NEWBURY AND ROWLEY

Lying in the northern portion of the Plum Island River the flats of Newbury and Rowley are less extensive than are those of the Merrimack River mouth. Part of Newbury is restricted by contamination but at least 30 acres of suitable clam ground remains available. Clam abundance is low here and no satisfactory explanation has been found for this. Plantings have been made in both towns for several years but have not met with complete success. Rowley's flats comprise a total of about 50 acres but production is as poor as it is in Newbury. Unusually large numbers of horseshoe crabs in the Plum Island River in 1948 have been observed by inhabitants of nearby towns,

and their predations may be partly responsible for the unsuccessful results of this year's clam plantings. Further study of the region is planned in 1949 by the State and by the U. S. Fish and Wildlife Service.

IPSWICH

The widening of the Plum Island River plus the confluence of two major tributaries give the town of Ipswich a clam area totalling some 800 acres. This is the source of the famous Ipswich Clam which is well known in many seafood restaurants. A small part of the area is affected by pollution from the Ipswich River but amounts to a negligible fraction of the whole. Clam abundance is low here but the outlook is encouraging.

During the summer of 1948 Ipswich began the imposing task of clearing large sections of its clam flats of the blankets of blue mussels which had accumulated over a period of several years. Fortunately removal operations in Ipswich were begun in time so that many living clams were found after the mussels had been cleared away. The problem of the blue mussel is acute in many localities, once productive clam flats have been inundated by it. Several methods for disposing of this shellfish "weed" have been devised but the one now in use at Ipswich has proved to be the most effective.

A war surplus landing barge was purchased by the town and equipped with a dredge similar to those used in the taking of quahaugs. Operations are conducted at high water over the infested flats, the musselsl being brought up and dumped into the bottom of the barge. When approximately 15 tons have been thus collected the load is transported to deep water and shovelled overboard. Between August and December of 1948 more than 15 acres have been thus cleared and clams are being dug on this reclaimed area. To date Ipswich is the only town in Massachusetts to conduct a determined campaign against the blue mussel and this action is to be commended. Such work is a necessary part of the campaign to restore the clam flats of the Commonwealth to their former state of productivity.

ESSEX, GLOUCESTER AND THE CAPE ANN REGION

The towns of Essex and Gloucester are contiguous and their clam grounds are located on the south shore of Ipswich Bay. Essex is the more important with regard to clam production, its flats covering more than 300 acres in comparison to Gloucester's 100. Essex has no pollution problem but Gloucester Harbor and part of the Annisquam River are closed because of contamination.

Both towns have always maintained commercial shellfisheries although they are at a low ebb due to the general shortage of clams. In the late 19th century Essex inaugurated the grant system which provided for the leasing of small tracts of the flats to residents of the town. This system never achieved great popularity in Essex but was subsequently tried with some success by other towns in the state.

In Provincetown one finds a large population which depends upon the fishing industry for its livelihood. During the winter many of these people count on shellfish to supply them with part of their food. If there are no shellfish the burden on town welfare is increased during the cold months. Commercial shellfishing would be limited to digging for town use in restaurants and hotels, which market is considerable during the summer. Recreational digging is not heavy in Provincetown.

In 1947 a good natural set of clams was observed and an area was closed to digging in order that the young clams might develop. An extensive planting of seed clams was made in 1948 under the direction of the Massachusetts Division of Marine Fisheries.

TRURO

Truro has never ranked high among the clam-producing towns of the Cape. In 1907 Belding lists only one man as digging clams there and the value of his catch was $60.00. Since that time Truro has enjoyed some successful years but the size of the flats is too limited to permit a large crop. Only three acres were listed as bearing clams in 1907 with 47 more considered possible to utilize. Recently changes in the circulation of water over one of the town's best areas has resulted in the covering of the flats with sand, transforming relatively stable beds into shifting sand bars and eliminating such clams as had been there.

A planting of 100 bushels of clams was made in the spring of 1948 and appears to be doing well. A limited amount of propagation in Truro would go a long way toward providing family and recreational digging for the townspeople and their summer visitors.

WELLFLEET

Belding's report on the mollusk fisheries shows Wellfleet Harbor in 1907 as teeming with quahaugs and scallops and the areas near shore staked out into oyster grants. Clams were there but in small numbers and scattering localities. The picture is similar today with all shellfish proportionately reduced, clams almost to the vanishing point. Clam culture has suffered from shifting sands which have played havoc with otherwise suitable flats. As Wellfleet is not primarily a clam town the situation is not as serious as it might otherwise be. Fortunately there is no pollution problem and scallops, quahaugs and oysters thrive in its waters.

EASTHAM

Forty years ago Eastham was first among the towns of Cape Cod in clam production. At that time Belding states that 36 men were digging commercially there and that the catch for the year 1907 was 4000 bushels. The area of good and fair digging comprised 75 acres with 200 more considered as

potentially productive. Since then the picture has changed and only a few acres of the extensive flats now harbor a remnant of the formerly abundant clam population.

Eastham has no trouble with pollution and, considering the area of the potential clam-producing flats it should be possible to provide family and commercial digging for the townspeople as well as recreation for summer visitors. As a small town, possessing no sea fishery, the value of the shore fisheries should be emphasized. Town income would be greatly augmented if the clam grounds could be restored to their erstwhile flourishing condition.

ORLEANS

Adjoining Eastham, Orleans closely resembles it in the size and general characteristics of its clam flats. Clams were dug in varying amounts on 75 acres in 1907, according to Belding, while an equal area was considered by him to have possibilities. In 1907, 30 commercial diggers took 3,000 bushels of clams from the town of Orleans.

Today overdigging appears to be partly responsible for a depleted clam supply but as in other Massachusetts coastal towns there are many further contributing factors. No pollution is encountered within the township but shellfish enemies such as horseshoe crabs and boring snails must constantly be guarded against.

Fishing, both sea and shore, represents an important source of income to the town of Orleans. There is a small fleet of draggers which operates in Cape Cod Bay and various species of shellfish provide food and occupation for many families. To the large summer population the clam grounds are a major attraction and tie in with the recreational aspect of the town's industries. The local demand for clams is sufficient to warrant a substantial investment by the town in order to increase the available supply.

CHATHAM

At the present time the widely dispersed flats of Chatham are bearing very few clams although the potential acreage is large. Belding's figures show that good digging could be found on 50 acres in 1907 and that 300 more might be made to produce. In that year 1500 bushels were taken and this amount was exceeded as recently as 1945 when 2382 bushels valued at $9528.00 were harvested. During the past three years, however, practically no clams have been dug commerically.

Chatham is one of the larger summer colonies on the Cape and supports several hotels. The demand for clams is great at all seasons but summer digging is especially heavy. Over 200 "guest" permits are issued each year, which, together with some 400 "family" licenses indicates a real local interest in non-commercial digging. It would seem, therefore, that Chatham's immediate problem is to build up its clam supply to the point where it is capable of meeting local demands before attempting to provide for outside consumption.

all. Scallops and quahaugs are far more important to the Falmouth shellfishermen as the waters of the town are better suited to their culture.

Two bodies of water suffer from pollution within the township but have been found useful as bountiful sources of seed quahaugs for transplantation to clean areas.

Falmouth has one of the largest summer populations, both resident and transient, of any town on the Cape and hence has the problem of supplying its visitors with shellfish for home consumption. Although suitable flats are limited, much could be done to better the present situation and provide recreational digging for summer residents and clams for the family use of permanent residents.

BOURNE

Lying on the eastern shore of Buzzard's Bay, the clam flats of Bourne are somewhat limited in extent. The mean tidal range is just over four feet and the character of the beach is not ideal for clams. Belding's report states that in 1907 scattering clams could be found on 30 acres of flats within the township and there were no areas where the clamming was considered good.

Like Falmouth, Bourne is primarily a quahaug and scallop town although there is sufficient suitable space to provide clams for family use.

A system was devised in 1942, whereby all holders of shellfish permits are required to make a monthly report to the shellfish officer stating the amounts and species taken. Post cards are provided for this purpose, the license holder filling out the brief form on the back of the card and mailing it to the warden. It is thus possible to check closely the amounts of shellfish taken from the waters of Bourne each year. In many ways the administration of shellfish matters in the town of Bourne could be taken as a model by other towns. The townspeople are apparently well aware of the value of their shellfisheries and are willing to invest town funds in an industry which brings such profitable returns.

THE NORTH SHORE OF BUZZARD'S BAY

Generally speaking the Buzzard's Bay region is not ideally suited to commercial clamming because of the limited extent of the flats. Quahaugs, scallops and oysters comprise the most important species and the many harbors, bays and rivers which indent the shoreline provide an ideal habitat. One of the principal factors limiting the abundance of clams in Buzzards Bay is the low tidal range. This feature is mentioned in connection with the towns of Bourne and Falmouth.

Of the seven towns which make up the north shore of Buzzards Bay, Wareham is foremost in shellfish production. Possessing a long shoreline and many tidal inlets an excellent shellfish habitat is provided. Large plantings of clams have been made annually and other propagation activities have been carried on. Sizeable appropriations are made by the town for this work each year.

Marion, Mattapoisett, Fairhaven, New Bedford, Dartmouth and Westport concern themselves primarily with shellfish other than clams. Quahaugs and scallops thrive in their waters and many oysters are to be found. Considerable pollution exists in the vicinity of New Bedford, affecting parts of Fairhaven and Dartmouth.

THE FALL RIVER - SWANSEA AREA

Of the six towns in this region none now produces clams in any quantity. This is due almost entirely to contamination by industrial waste and domestic sewage from the towns bordering the Sakonnet and Taunton Rivers. In 1907, 5000 bushels were taken from Swansea while Somerset, Dighton, Berkley, Freetown and Fall River contributed smaller amounts. Oysters are now the principal shellfish resource of these towns. Approximately 200 acres of clam flats are available for productions when the present sources of pollution are eliminated.

MARTHA'S VINEYARD ISLAND AND NANTUCKET

Lying off the south shore of Cape Cod where the rise and fall of the tide is limited, "The Islands" are in much the same category as Buzzards Bay and the southern Cape shore. Exposed as they are to the open sea all clam flats must, of necessity, be located within the shelter of tidal inlets and bays. Circulation in most cases is limited and environments are not of the best for soft-shell clams. What has been written about the towns of Buzzards Bay concerning their shoreline applys to Martha's Vineyard and Nantucket.

There are six towns on Martha's Vineyard of which Edgartown has the largest shellfishery. This consists principally of the quahaug and scallop industry carried on in Katama Bay and the Great Pond. The other towns, Oak Bluffs, Tisbury, West Tisbury, Chilmark and Gay Head are essentially similar, but do not control waters as extensive as those lying within the township of Edgartown. The Great Ponds, situated just inside the south beach of the island support a small clam population but are better suited to oysters which are cultivated with some success in Chilmark and West Tisbury.

Nantucket controls some of the most extensive shellfish areas in southern Massachusetts and derives a considerable income from the annual catch of scallops and quahaugs. Extensive areas are available for clam culture which, if developed, could bring in a substantial revenue to the fishermen of the town. Good crops have been produced in the past and restocking activities are contemplated for the spring of 1949. Generous appropriations are made by the town each year for shellfish work.

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List of Contributions

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